A NOTE ON THE DISTRIBUTION OF THE VULTURINE FISH-EAGLE, *GYPOHIERAX ANGOLENSIS* GMEL.

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EVERY student of African birds must have been struck by the anomalous distribution of *Gypohierax angolensis*. Bannerman, the latest authority (**2**, p. 272) states that the bird occurs "in Western Africa almost universally from Gambia to Angola," but "its occurrence in Eastern Africa is most irregular, recorded, as it is, from Niam-niam[1], the Usambara Mountains in Tanganyika Territory, Lake Nyasa, once from the Transvaal, and once from Pemba Island in the Zanzibar group." The Transvaal bird is said to have come from Potchefstroom (**5**, p. 604). This record seems to have remained unique for many years, although much ornithological work has been done locally, and it evidently refers to a rare straggler. In Pemba, on the other hand, the bird is "common all round the coast," though it is "rare on the mainland coast," and, surprisingly, "it does not occur in Zanzibar," the sister island (**7**, p. 604). The "mainland coast" referred to is that of the Usambara; Pemba, Zanzibar and the Usambara Mountains, where this was written, all being within sight of each other. An excellent map showing the relationship of the Usambara Mountains and Pemba Island appeared in the *Ibis*, 1932, facing p. 492.

As regards the status of *Gypohierax* in Usambara, the experience of several years has led me to conclude that even within that comparatively small area it is restricted to a particular locality. This locality is not, as might be expected, along the coast, or the chief river of the region; but in the immediate neighbourhood of the Middle Sigi Valley, a trench-like feature between two blocks of the East Usambara Mountains. With its bed only 500 ft. above sea-level, and its sides rising to 3500 ft., this valley experiences temperature and humidity in combination probably more consistently high than in any other locality on the East African mainland. It still contains much evergreen forest of a type almost entirely destroyed elsewhere. There is no record of *Gypohierax* from the Usambara Mountains except those overlooking the Middle Sigi Valley, among which Amani is situated, and I can confirm Vaughan's allusion to its rarity on the coast. At Tanga, which is midway between its two permanent stations, Pemba Island and the Middle Sigi Valley, and hardly 40 miles from

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[1] Niam-niam is the north-east edge of the Congo basin, and within the West African rather than the East African region.

either, I have never seen it. There is, moreover, no record from Kenya Colony, so well worked ornithologically by Dr Van Someren and others, although the border is only 50 miles to the north. In fact, notwithstanding its great powers of flight this bird is localised very narrowly and in a peculiar manner in East Africa, even within the restricted area to which the published records refer.

In West Africa *Gypohierax* occurs all along the rivers and creeks, utilising especially mangroves. In Nigeria "almost any patch of rather large trees by water is likely to hold it" (Hutson *cit.* Bannerman). Such conditions are forthcoming throughout a large part of the East African coast, from which the bird is absent. At first sight its food requirements are equally unspecialised. It is "a scavenger by nature, and besides eating fish it has earned for itself the reputation of being a bold rapacious bird which attacks living prey" (**2**). In Pemba it "feeds largely on offal and various forms of marine life picked up round the shore" (**7**).

My first impression was that in the Amani district the Vulturine Fish-eagle led an uncertain and wholly predatory existence. There are few fish of any size in the local mountain torrents and no collections of offal such as are provided along tide-mark. During two years the information collected of its local feeding habits was that it had been known to harry monkeys (*Cercopithecus albigularis* Sykes), kill and eat poultry and a full-grown domestic cat. Snails also had been found in one stomach, and in another a mass of much-digested fibrous material which baffled identification. On this basis when in 1930 I wrote some field notes of the bird (**6**, p. 501) I was quite at a loss to suggest a reason for its localisation to the Middle Sigi Valley.

Vaughan, our only East African authority, does not include any vegetable element in *Gypohierax* diet. In West Africa, however, according to Bannerman, "naturalists agree that its favourite food when in season is the kernel of the oil palm" (*Elaeis guineensis* Jacq.). Now there are at Amani plantations of oil palm started by the Germans probably about 1910, and elsewhere overlooking the Middle Sigi Valley there is a plantation said to date from the 1890's. Since writing my field notes, I have had the opportunity of examining two more Amani *Gypohierax* stomachs, both of which were found to contain oil-palm fruit to the exclusion of other food. Moreover the acquaintance thus gained with the appearance of oil-palm fruit in a half-digested condition led to a realisation that the macerated fibre previously encountered in a *Gypohierax* stomach came from the same source.

This showed that the extremely isolated East African colony retained the ancestral preference for palm kernels. It led to enquiry as to the published distribution of the palm. Engler (**3**, p. 234) gives it as Senegambia and Angola and east to the Niam-niam, the banks of Lakes Tanganyika and Nyasa, and "introduced on the coast of East Africa especially in Pemba." It will be observed that the limits thus indicated agree almost word for word with those for *Gypohierax*.

Mr P. J. Greenway, Botanist at this Research Station, has very kindly examined the literature for me, and it appears that the East African localities given for the ("introduced") oil palm are Pemba, Zanzibar and one or two spots on the opposite coast. Mr Greenway has recently made a botanical survey of the Zanzibar Protectorate and he informs me that the status of the oil palm in the two islands is quite different. In Pemba the palm is an important element in swamp forest all along the west coast of the island and, although material collected previously has been put under *Elaeis guineensis* Jacq., he considers that it is a distinguishable form, undoubtedly indigenous. In Zanzibar on the other hand oil palm was found in a single spot only, the Yosani swamp. Vaughan with two more years' experience of Zanzibar Island since his field notes were written informs me (*in litt.*) that he has still no record of *Gypohierax* in that island: he has not visited Yosani. It may be remarked in passing that the two islands, Zanzibar and Pemba, have very different geological histories, and faunae and florae in many respects distinct.

The ranges of *Gypohierax* and the oil palm in one form or another are thus shown to exhibit at the present day a remarkable coincidence. (Cf. Reichenow (*op. cit.*): "Bohndorff fand den Geierseeadler in Niamniamland überall wo die Ölpalme vorkam.") It appears that this must mean either that they have identical climatic requirements or that the bird is actually dependent on the plant. On the whole the former is unlikely. Vaughan gives a convenient summary of the Protectorate climate. The daily mean maxima are 84·5° F. for Zanzibar and 86·6° F. for Pemba, the minima 76·5° F. and 76° F. respectively. Both climates are very equable. It is difficult to believe that the small differences between them can be significant in determining the distribution of the bird.

Although the facts thus pointed to the direct dependence of the bird on the palm, there was at this point one flaw in the completeness of the connection between them. It lay in the fact that Kirk's Usambara specimen was collected about 1880, while according to local information the earliest oil palm plantation in the Usambaras was not started till nearly 1890. This is probably correct, as European settlement did not begin till 1884. If the oil palm was so recent an introduction it struck me as peculiar that the local natives had a well-known name for the plant which appeared to be good Bantu. Language authorities I consulted, particularly Canon Hellier of the U.M.C.A., confirmed the impression that MCHIKICHI appeared in the earliest dictionaries of the local languages and that the word bore no indication of being a secondary formation. It might have been derived from "Ki-pemba," or its prevalence might indicate that a form of the oil palm was indigenous to the Usambaras. I was therefore encouraged to make a search for a wild oil palm locally. The Middle Sigi Valley with its humid tropical climate appeared suitable, and there in the surviving forest an *Elaeis* was found growing under apparently natural conditions. The material collected was insufficient for complete identification,

but Mr Greenway thought that it might be identical with the Pemba form. Therefore, it appears that, besides the imported West African *Elaeis*, there may be a native East African form on the mainland, its station being the site of the relict colony of *Gypohierax*.

Evidence in favour of a hypothesis that the Vulturine Fish-eagle is dependent on the oil palm is thus fairly complete. The question now arises as to the nature of the connection between them. The possibilities are either that the palm supplies an essential physiological requirement, or that it merely satisfies a taste-preference. The peculiar properties of the oil-palm fruit make it likely that the first alternative is the correct one. Recent biochemical work has shown that "red" palm oil, as found in the raw fruit, is a remarkably rich source of vitamin A (4). Evidently when one of the birds fills its stomach with the fruit it must ingest an enormous dose of the vitamin.

It may be recalled that Bannerman refers to the bird's preference for "the kernel of the oil palm" when "in season." In view of the bird's close restriction throughout the year to the district in which oil palms occur—in East Africa at least—it is of interest from the theoretical point of view to know to what degree the supply actually is periodical or intermittent. The literature on oil palm appears to contain very few references on this point. However Adam (1, p. 116) remarks: "Les régimes se forment à toute époque de l'année. Cependant il existe des saisons ou ils naissent en plus grand nombre; c'est pendant les saisons pluvieuses." An exactly similar remark is applicable to the introduced oil palms in the Middle Sigi Valley: and such evidence as is available for the presumptively native form of oil palm in Pemba indicates that it also bears more or less of fruit all the year round.

Without properly controlled experiments it could not be established whether frequent large doses of vitamin A, such as *Gypohierax* evidently obtains under natural conditions, are essential to its life. The practical difficulties would be considerable. It occurred to me however that general experience in captivity might be suggestive. I therefore applied to the Secretary of the Zoological Society of London for information regarding the diet and survival of *Gypohierax* in the Gardens. He kindly replied as follows: "We have had only a relatively small number of Angolan vultures here, and over a period of 25 years, of which I analysed the figures some time ago, we had 12. Their average duration of life was 40 months, and the one that lived longest lived only 5½ years. Both the average and the maximum duration are very much less than that of the other vultures in our Collection. I find that they were fed just like the other birds of prey, and certainly had nothing like palm-kernels."

Climatic factors might, of course, have been responsible wholly or in part for this specifically high mortality. I understand that vitamin A will be specially added to the birds' rations in future. We may expect that, in the course of years, satisfactory evidence will be accumulated on the point at issue.

Whatever the outcome of feeding experiments the facts given above go far towards proving that a highly aerial bird, and one with a particularly varied diet, may be tied closely and perennially to the immediate neighbourhood of a food that makes only occasional appearances in the stomach. The result is of some theoretical importance in the study of animal distribution.

SUMMARY.

The West African vulture *Gypohierax* appears in East Africa only in Pemba Island and East Usambara. In West Africa it is well known that oilpalm fruit is a favourite element in its mixed diet and that the limits of bird and palm correspond. Oil palms, hitherto all regarded as introduced from West Africa, occur in Pemba and Usambara, and there also *Gypohierax* eats the fruit. Actually an indigenous form of oil palm appears to be present. Thus the bird's anomalous range agrees throughout with that of the palm. Crude palm oil is very rich in vitamin A. Several *Gypohierax* kept in the London Zoo without special vitamin A supplement have been shorter-lived than the other vulturines.

Note. The above was accepted for publication on December 12th, 1932. Since then I have through the kindness of Dr J. P. Chapin received a copy of his magnificent "Birds of the Belgian Congo" (Part i), *Bull. Amer. Mus. Nat. Hist.* vol. 65, which was published on December 17th, 1932. In the article therein on *Gypohierax* (pp. 520–3) he gives striking evidence of the detailed connection between the bird and the oil palm in the Congo. R. E. M.

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FLUCTUATIONS IN NUMBERS AMONG FRESHWATER CRAYFISH, *POTAMOBIUS PALLIPES* LEREBOULLET

By J. E. DUFFIELD.

(*With Plate V.*)

I. INTRODUCTION.

THE object of the present paper is to draw attention to the fluctuations which occur in the numbers of freshwater crayfish, and to give some evidence about their periodicity in the Rivers Ock, Thame and Windrush, in the Oxford region. The crayfish is usually very common in the streams around Oxford, especially within that triangle of hills formed by the Chilterns, the Cotswolds and the Berkshire Downs. As it is an object of sport and is often caught on fishermen's hooks, past fluctuations in its numbers are likely to have attracted attention and a good deal of information has been obtained about them by local enquiries. The crayfish belongs to a class of animals which has seldom been studied from the present point of view. Goodrich (6) has, however, examined similar fluctuations in the freshwater shrimp, *Gammarus pulex*, near Liverpool and Oxford, and has proved the occurrence of epidemics due to protozoan organisms.

It has to be borne in mind that when an observer says crayfish died out in such and such a year in such and such a district, this date may refer only to a limited area in the district, as far as he knows. But when after a year or two the crayfish disappear throughout the whole area he concludes that they have all disappeared in the same year, whereas such may not have been the case. Care has been taken to eliminate this pitfall, but the attempt may not always have been successful. Such possible errors have prevented conclusions from being drawn about the rate and direction of travel of the periodic reduction in numbers.

The evidence summarised below, together with what is known about crayfish on the continent of Europe, shows that crayfish fluctuate with considerable violence, and that epidemic disease is probably the main cause. Biological evidence shows that the popularly supposed causes such as pollution are not important.

In collecting evidence on the subject it was found that millers, fishermen and farm labourers gave the most valuable information, and were usually able by association to fix the past dates with surprising accuracy. Questionnaires were sent to various people but were not nearly so successful as personal

interviews. The writer records his thanks to the many observers without whose co-operation the present work would not have been possible. In particular thanks are due to Charles Elton for much valuable advice.

II. FLUCTUATIONS IN THE OXFORD DISTRICT.

Three rivers have so far been studied: the Ock, the Thame and the Windrush.

(a) The Ock.

The Ock is a tributary of the Thames which it enters at Abingdon, after a course of some 25 miles through clay soil. The water is hard from calcium carbonate but is otherwise free from pollution, except from tar and oil derived from the roads—a factor less marked in the Ock than in most other rivers owing to the rural nature of the land through which it flows. The river is divided into sections by a number of mills (now mostly disused and causing considerable blockage by their dilapidated condition) which act as barriers to the free dispersal of water animals. During periods of abundance crayfish occur throughout the whole length of the river and in many of the side streams provided they are not too stagnant. They are most plentiful in stretches of the river which flow north and south; the reason for this, according to Huxley (**10**), is that they get less sun under the banks in these stretches than in other parts. The crayfish live in holes in the bank sometimes at a depth of 8 ft., but more commonly from 2 to 4 ft. below the surface.

1880–1887. From Cutts Mill, Abingdon, to the "Noah's Ark," Marcham. Abundant. Could catch two sackfulls in an evening between 6 p.m. and 11 p.m. Have seen as many as four sacks taken by a party. The "game cart" used to be employed to carry the crayfish back to the village. The frontage of one field only was fished at a time as a rule. In 1887 and three or four following years not a single crayfish was caught. Disappearance attributed to pollution. (C. J. Duffield, Marcham.)

1881–1884. Cutts Mill, Abingdon, and district. Plentiful between these two dates. Catch "a couple of bucketfulls in half an hour." Disappeared about 1885. The disappearance coincided approximately with a fungus disease among such fish as roach and chubb.
(C. C. Cheer, Cutts Mill, Abingdon.)

1884—1885–8. From Garford to Stanford-in-the-Vale. Plentiful about 1880 or a little afterwards; disappeared suddenly one year between 1885 and 1888; cannot say which. Did not reappear during three following years, at least; after which crayfishing was abandoned. Fish became scarce about that time or later. Crayfish epidemic attributed to pollution.
(Dandridge, E. Hanney, near Abingdon.)

1884–1887. "Noah's Ark" to above Garford, including side streams. Plentiful during three years. "Could catch in an evening more than could be wheeled in a barrow." Disappeared in 1888 and for following few years at least. (W. Hazel, farm labourer, Frilford.)

1886. Stanford-in-the-Vale to below Marcham Mill, including side streams. Plentiful in this and the few preceding years. None in 1887. Fish definitely not affected at the same time. None in next two or three succeeding years at least. (W. West, miller, Drayton, near Abingdon.)

1886. Marcham Mill and a quarter of a mile on either side. Plentiful about 1886 but disappeared suddenly about that time. (R. Fathers, Marcham.)

1889. Marcham Mill and district. Crayfish died out sometime at the end of the "eighties." (Informant very vague of even approximate dates.) (J. Thomas, labourer, Marcham.)

Of the seven informants mentioned above, all agree that crayfish were plentiful at the beginning of the "eighties" and remained so until at least 1885. The crayfish disappeared before 1890. 1887 seems to be the most likely date of the disappearance, at least for the lower reaches.

1900. Garford district. "A few at beginning of century" (twentieth century) but died out about 1903. (J. Lawrence, labourer, Marcham.)

1900. Below Marcham to Cutts Mill. A few taken on hooks while fishing. None caught after 1903 approximately. (T. Brewerton, professional fisherman, Abingdon.)

1900. Abingdon Common and district. A few crayfish in main stream and side ditches. "Could catch as many as could be carried on a bicycle in a sack." Had disappeared by 1903 or 1905 at latest. (J. Stone, herdsman, Abingdon Common.)

Evidently a few crayfish were inhabiting the Ock at the beginning of the present century. The fact that they were not so abundant as in the "eighties" is confirmed by their being observed by so few people in spite of the more recent date.

1910–1913. Garford, Hanney and Marcham. Some were caught in 1910 and for the next year or so they disappeared either in 1912 or 1913. (W. West, miller, Drayton.)

1912–1913. Abingdon Common and District. A few crayfish were caught in 1912 but there were none in 1913. Have always been a few in side stream of Ock running under Abingdon Road. (J. Stone, herdsman, Abingdon Common.)

A disappearance occurred in 1912 or 1913, but was evidently not sufficiently large to attract notice.

1923–1930. Garford to Stanford-in-the-Vale. Plentiful in 1923 and 1924. "Swarms in 1925 and 1926." All died out by 1928. "Could catch more than two men could carry in an evening." None since. Disappearance attributed to pollution from factories.

(Reed, "Station Inn," Abingdon.)

1924–1930. Cutts Mill, Abingdon, to "Noah's Ark," Marcham. Crayfish were very abundant in 1925 and 1927, also to lesser extent in 1924. There were none in 1928 nor have there been any up to the present (1930). (J. E. D.)

1926–1930. The whole Ock from Abingdon to source. In 1926 and 1927 crayfish were plentiful all up the river. "In an evening's crayfishing, many were put back into the water as more were caught than were required." In 1928 there were none below "Noah's Ark," Marcham. In 1929 they had disappeared from the whole river. Epidemic attributed to pollution. (Ward, Westminster Bank, Abingdon.)

1927 and 1929. "Barnstaple Brook," side stream of Ock at Marcham. Plentiful in 1927 and 1928. In 1929 hardly any. The informant believes that regular epidemics, due to overcrowding, occur every ten years. (P. W. Aldworth, farmer, Marlborough; W. Hazel, labourer, Frilford, confirms this.)

1929. Side stream of Ock crossing Frilford Golf Course. A few large crayfish can be seen in this stream. (W. Steptoe, carpenter, Frilford.)

1927–1928. Garford, Hanney and Marcham. Plentiful in 1927 and few years previously. None in 1928. (W. West, miller, Drayton.)

This date is in disagreement with other observers. (J. E. D.)

1923–1929. Garford to above Hanney. Plentiful until 1927, just as in "eighties" of last century. Disappeared in 1928, a few surviving until 1929—these chiefly in the side streams.
(Dandridge, miller, E. Hanney district, near Abingdon.)

1921–1930. Garford and Hanney district. Abundant until 1927, few and small in 1927. None in 1928. The observer believes epidemic was due to overcrowding. He says fish in Ock were killed by pollution from Wantage several years ago, but dace and trout increased in 1920 and 1929. (Capt. Budgett, Hanney.)

1930. During 1930 the author questioned thirty-seven fishermen along the banks of the Ock about the recent disappearance in 1928. The results obtained were as follows: five had no knowledge of crayfish; three held the crayfish were hibernating (although it was early September); twenty-three held that an epidemic occurred in 1928 all up the river; six held that an epidemic occurred in 1928 in lower reaches, 1929 in upper reaches.

From the above, it seems that there were crayfish in abundance from about 1924 until 1927, when they suddenly disappeared[1]. Concerning this recent disappearance no doubt whatever exists, and for this reason the author has refrained from multiplying tedious repetitions.

In 1884 these Crustaceans were extremely abundant in the River Ock and sackfulls could be caught in the course of an evening. This continued until September, 1887, when not a crayfish could be caught anywhere in spite of several attempts. This dearth of crayfish persisted for several years, after which crayfishing was not tried. Crayfish were caught for a year or two in small numbers in 1903 and again in 1913. There is no record of their having been caught between these two dates. In 1924 crayfishing was again tried, following reports of anglers who had caught them on their hooks. It was found that crayfish had returned in as great an abundance as in 1886. Exactly when they returned it is unfortunately impossible to say, as they usually pass unnoticed until they are fairly common. They were still abundant in 1927, and from a short stretch of river, perhaps 100 yards long, it was possible to fill a sack in a few hours. In 1928 there were no crayfish in the lower reaches of the Ock, although they persisted further upstream. But in the following year, 1929, they had disappeared from upstream also.

After this recent epidemic crayfish were still to be found in a few of the side streams, but only in small numbers. The survivors were mostly large, and therefore old, crayfish. During 1931, reports of fishermen indicated that crayfish had again reappeared in the Ock but that they were not at present very numerous.

Discussion. The conclusions to be drawn from these facts will now be discussed before proceeding to examine how far other rivers bear out the theory of periodic fluctuations in numbers. Dates of maximum abundance

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[1] At the present time (July, 1933) a few crayfish have reappeared in the Ock about a quarter of a mile above Marcham Mill. (J. E. D.)

were about the years 1886 (? 1900), 1911 and 1927. We suggest that a peak year (i.e. a year in which crayfish are at their maximum abundance) probably occurs about every 13 or 14 years, and that these peak years are followed by a sudden disappearance of the crayfish. Presumably when they exceed a certain density an epidemic takes place. Their disappearance may be due to epidemic disease, migration or pollution, and it will be shown below that the last two of these are unlikely causes. Now if the theory of periodically recurring epidemics is correct, two things necessarily follow: firstly, we should be able to forecast with fair accuracy the numbers of crayfish in different years; and, secondly, it should be possible to confirm the work on other rivers. As regards forecasting, the work was only begun in 1927 and therefore has not been in progress long enough to test the results. However, the fact that crayfish are now returning to the Ock after their recent disappearance is in keeping with the above view.

The only other two rivers which have so far been investigated also confirm the theory, and these we shall now discuss.

(b) *The Thame.*

1886. From source to entry into the Thames, including side streams. Crayfish plentiful in 1886. Disappeared in 1889 and had not returned before 1894. There were plenty in 1900 but not so many as in previous years (i.e. before 1889). These disappeared in 1904 or 1905. Local theory has it that the water was contaminated, but this observer does not think so. There are now (1930) plenty of crayfish just as there were before 1889. Simultaneously with the epidemic of 1889 there was a heavy mortality among fish of nearly all sorts. The fish showed "a virulent ulcer or cancer on side of belly." (E. L. Franklin, farmer, Brookhampton, near Oxford.)

1900. Shabbington and Ickford district. Crayfish abundant in 1900. "Could catch half a sack in less than an hour." Died out a few years later, that is about 1904 or 1905. They had reappeared about 1914, but there was another disappearance in 1918. The explanation given for the later (1918) disappearance is that the watercourses were choked with weeds. Crayfish are now plentiful in the district. Fish, though at present (1930) scarcer than before 1914, are said not to have disappeared simultaneously with the crayfish. (Above information was collected by the writer from two old inhabitants at Ickford.)

1915. Shabbington to above Thame. Plentiful about 1915. Disappeared in 1918. After this date the river was restocked and crayfish are now (1930) plentiful.

(Shabbington Inn.)

1880. Shabbington and just below, to above Thame. Plentiful in 1880 but all disappeared in 1889. No crayfishing was attempted until 1915, when a few were caught, but these died off again in 1918. There are now (1928) plenty of crayfish. (W. Ashurst, Waterstock, near Oxford.)

1930. The author questioned eighteen fishermen along the banks of the Thame during the summer of 1930. The results were as follows: two knew nothing of crayfish epidemic; one denied anything in the nature of an epidemic but said crayfish were liable to fluctuations; three remembered an epidemic between 1885 and 1890, and one in 1918; five remembered an epidemic between 1902–1905 and one in 1918; seven remembered an epidemic in 1918. All agreed crayfish were now abundant in the Thame.

Photo. J. E. Duffield

The River Ock above Marcham Mill.

DUFFIELD—FRESHWATER CRAYFISH

Crayfish disappeared suddenly from the Thame in 1889 and the few preceding years were years of abundance. They had reappeared by 1915 and again had an epidemic in 1918, but they are now very plentiful in the river. The writer has not been able to get evidence relating to their numbers in the early part of this century. Thus we have for the Thame two records of epidemics at an interval of 29 years; that is, roughly twice the interval between epidemics in the Ock. If we suppose an epidemic in about 1905, we should obtain a cycle roughly corresponding in length with that of the Ock. At present we have no information about crayfish numbers at that period.

(c) *The Windrush.*

1893. Witney—New Bridge. Plenty of crayfish before 1893 and previous few years. None caught in 1894. They are now (1929) plentiful again. The cause is attributed to the absence of a certain weed (which weed is not known). This disappeared with the crayfish. The weed and the crayfish have returned during the last three or four years, i.e. in 1925 or 1926. In 1915 fish of all kinds were found floating dead down the stream, the cause of death or whether crayfish were affected does not appear to be known by the observer.

(G. E. Holtom, Ducklington Mills, Witney.)

1895–1898. Burford to Bibury. Plentiful about 1895. "Were swept away" by 1898. They are now (1930) plentiful again. The observer has introduced them to the river.

(A. Sevem, Bibury, near Fairford, Glos.)

1897. Witney to above Burford. Present previous to 1897 in large numbers. None in 1897 until 1902 when a few were taken. They had disappeared in 1903. At present (1929) they are "excellent in numbers and quality." Epidemics attributed to pollution.

(A. Eustace, Burford.)

1898. Burford to Barrington. Abundant in 1897 and previous years, but disappeared in 1898 until 1903, when some were caught. In 1905 or 1906 they disappeared. Some were caught in 1915 but those died off in 1918. They were abundant in 1930 and could be caught "by the sack." (Landlord of "Fox Inn," Burford.)

1913. Burford district. A few caught on fishing hook in 1913 and for next few years, but none after 1918. Now, in 1929, very plentiful. (J. Down, Burford.)

Crayfish were plentiful in 1893 and disappeared in 1894. They returned in small numbers by 1902 and disappeared again in 1905. A fair number were caught in 1915 but there were none in 1918. At the present time (1931) they are very abundant. It is a remarkable fact that the epidemic seems always to spread *upstream*. Thus in Witney district the crayfish disappeared in 1894, but above Burford, at Bibury, they died in 1898.

III. FLUCTUATIONS IN OTHER RIVERS.

So far a detailed investigation of the evidence about other rivers has not been practicable. A search in the Natural History section of the *Victoria Histories of the Counties* (16) revealed the following significant records.

Berkshire.

"Crayfish have died out in the upper Kennet from an unknown cause." (Published 1906.)

Essex.

"The crayfish used to be common and probably is so still in the Lea and Chelmer; it is found in some streams of the New River Company in prodigious abundance. But Mr Fred Fielding says that the River Colne which used to be full of them (crayfish) no longer contains any (March, 1903)."

Now the only epidemic among crayfish of which the Ministry of Agriculture and Fisheries possesses any record is that of an epidemic in the Colne in 1927. Therefore, crayfish must have returned to the Colne by 1927. Presumably the 1927 outbreak was a fairly severe one, or it would not have found its way into the records of the Ministry of Agriculture and Fisheries.

Nottinghamshire.

"Crayfish are almost certainly subject to some limitations and fluctuations. The latter are apparently due to some epidemical disease or other temporary and local disasters. The former may be traced to uncongenial conditions of soil and climate.... It certainly does not occur in the Trent, nor in the district of Averham near Newark, but it is fairly common in the river Maun and in mill dams at Mansfield." (Published 1901.)

Yorkshire.

For Yorkshire the writer speaks of a "former abundance and present (1900) scarcity in the River Aire, near Skipton"; he says, further, "it also occurs in the Yore at Hawes where it may have been introduced from the Doe. It was abundant in the Yore when others were persecuted and is rare now when others are preserved." Smith (**14**) also records evidence of occasional sudden decrease in certain areas.

Thus it appears that crayfish epidemics occur in many parts of the British Isles. It is unfortunate that the Oxfordshire volume of the *History of the Counties* has not yet appeared.

IV. Factors regulating numbers of crayfish.

(*a*) *Disease.* The English crayfish, so far as is known, belong to one species only, *Potamobius pallipes* Lereboullet. On the Continent, however, there are two species at least which are commonly recognised, *P. torrentium* (Schrank) and *P. fluviatilis* Auctorum; both are of rather larger size than the English species (**15**). The crayfish is used extensively as an article of diet in France and Germany, and is accordingly cultivated on a commercial scale. In these two countries we have records of an epidemic occurring last century in 1878 (**3**), and according to a contributor in the *Fishing Gazette* (**1**) another one has recently occurred in Germany. There are insufficient records to give any clue as to whether these epidemics occur in cycles, and in any case the cultivation of crayfish on a commercial scale with its consequent heavy netting and restocking would almost certainly obscure such a cycle if it did exist. But the occurrence of the epidemic on the Continent has been mentioned because it is there that the specific cause has been investigated most thoroughly. In 1898

Hofer of Munich succeeded in identifying a bacillus which was associated with the disease (**9**). He named it *Bacteria pestis astaci*; it is an intestinal bacterium due to the pollution of water by sewage and industrial wastes. But in 1892 Henneguy and Thelohan found in the muscles of diseased crayfish the microsporidian, *Thelohania contejeani* Henneguy, and part of their description of diseased specimens runs as follows: "Ces muscles étaient, a l'état frais, blancs et opaques, comme ceux des Palaemons et des Crangons maladies" (**7**). Minchin (**11**) refers to *T. contejeani* as a "highly pathogenic species" and "a cause of the destructive epidemic among river crayfish in parts of France." But Doflein takes the view that the organism discovered by Hofer is the more probable cause of these epidemics. He writes as follows: "Vielmehr haben die neuren Untersuchungen von Hofer gezeigt dass die Krebspest eine Bakterieninfektion ist" (**4**). Thus the opinions of experts by no means agree as to the cause of the disease. A possible explanation seems to be that both *B. pestis astaci* and *T. contejeani* are the cause of diseases in crayfish, and that while the protozoon is the crayfish's natural parasite, the bacterium is a new parasite propagated by river pollution from the various causes associated with advancing civilisation. There is not much literature on the subject, and although German, Austrian, Italian, French and Russian scientists have contributed to the knowledge of the disease, no English scientist has worked on it, and the cause of the epidemics in this country remains to be investigated. Goodrich (**6**) has worked on *T. mulleri* in *Gammarus chevreuxi* and finds it to be the cause of epidemics in this crustacean. Henneguy and Thelohan have also proved the genus to be pathogenic to the shrimp Palaemon (**8**).

So far the author has been able to obtain only one piece of information as to the cause of the disease in England. He was informed that some crayfish which had been kept for several years in an artificial pond at Tubney, near Oxford, had "turned white and died." This whitening is a symptom characteristic of infection by *T. contejeani* in crayfish according to the above-mentioned authorities. Unfortunately it was too late to obtain the diseased specimens when the information was received. It can only be assumed then that the crayfish disease in this country may be due to infection by one or other of the above-named organisms and the only direct evidence so far obtained points to *T. contejeani* as the more likely of the two. But in view of the obscurity which envelops the whole subject, it seems best to keep an open mind until further work has been done on it. The chief difficulty in the way of elucidating the cause lies in procuring diseased specimens.

(*b*) *Pollution*. This is the popular cause to which deaths amongst crayfish and ordinary freshwater fish are attributed. When examined at all closely it is usually found to be inconsistent with the known facts, and to rest on the slenderest of evidence. The opening of gas works and factories, the advent of road tar and the consequent pollution of rivers with oil, do not coincide at all closely with any known crayfish decreases. Moreover, in spite of efforts to

prevent it, the pollution of rivers has increased of late years; and yet in two of the three rivers discussed above crayfish are at the present time extremely abundant. In the third river, the Ock, they were abundant only a few years back. If it were possible to account for the disappearance of crayfish at a certain date by the opening up of some commercial enterprise which caused a pollution of the river, their reappearance in large numbers at a subsequent date would not be consistent with the view. The above statements apply only to the idea that the crayfish are killed by chemical poisoning due to the pollution. Hofer (**9**) maintains that *B. pestis astaci* is associated with pollution, and if this is so it may be that the cycles in crayfish numbers are of comparatively recent date, the epidemics being accounted for by a variation in immunity discussed in Section (*e*) on "Climate, parasites, and starvation."

While discussing pollution, sheep dips deserve mention in view of the widely held notion that they are the cause of deaths among freshwater animals. That sheep dips contain arsenic and are powerful poisons admits of no doubt, and they are certainly used in dams by the side of rivers, the solution being discharged into the main stream after use. They might prove fatal to all animals within a certain area, but they could scarcely account for disappearances extending over several miles of river (except possibly in times of extreme drought, and decrease does not often happen to coincide with drought years). Moreover, sheep dips are used annually, and if they were the cause of the decrease one would expect the crayfish to die out annually, or to disappear completely.

The conclusion that we reach with regard to pollution as a cause of destruction is that, although the theory may be superficially attractive as an explanation, a more careful examination makes it untenable.

(*c*) *Enemies.* Crayfish, like other animals, have a certain number of natural enemies other than man. In his book on the crayfish Huxley (**10**) says that the trout is especially destructive to the young; this is confirmed by Pentelow[1] who found them in 27 % of trout stomachs examined in the River Itchen. The water rat is also partial to the crayfish. Probably most freshwater fish eat them regularly, at least they may be caught on hooks baited with the tails of crayfish. Duck are said to devour them, although whether they really do so to any large extent seems to be doubtful. The ravages of enemies could certainly not account for decreases such as those mentioned above. But when crayfish are scarce the effect of enemies, if at all numerous, might be appreciable, although once the crayfish have become numerous their effect can be but slight. It may be mentioned further that crayfish are usually abundant for several years before a decrease takes place, and it does not seem feasible that such a sudden reduction of the population could be accounted for by enemies.

[1] J. Animal Ecology (1932) 1, 103.

(*d*) *Migration*. At the present time when much work is being done on animal migrations, it seems fitting to consider whether migration might not provide a solution to the crayfish problem. The possibility of a crayfish migration has been suggested by several correspondents but none has so far produced any evidence in support of the idea. That crayfish should migrate as the result of overcrowding seems not improbable, but there is the difficulty of finding anywhere to migrate to. It has been mentioned that at times of abundance the river and side streams are full of crayfish, but there is not as a rule any direct water connection between two rivers by means of which crayfish could travel from one to the other, except possibly in times of flood. Also, as has been noted above, the powers of distribution of the crayfish are slight. But an observer in Yorkshire who kept crayfish in a pond in the garden records finding one of them at the door of his house 80 or 100 yards from the pond (**12**). We cannot however accept migration as an explanation until some evidence has been obtained to support it. As a matter of fact the powers of dispersal of the crayfish appear to be extremely slight (**12**), and after the severe epidemic of 1887 they do not appear to have returned to the Thames, where formerly they were plentiful although not so numerous as in the smaller rivers. Why they should not have returned is unexplained. In the Ock crayfish did not return to that stretch of water between the Mill at Marcham and Cutts Mill at Abingdon, when they were abundant above Marcham. Here the Mill, around which there is a very considerable amount of blockage, seems to have acted as a barrier to their spread downstream.

(*e*) *Climate, parasites, and starvation*. The author believes that in the joint action of these three factors the solution of the problem is to be sought. It is clear that summer conditions in rivers are usually more favourable than winter conditions, so that the summer increase caused by breeding ultimately reaches a point at which the following winter environment is unable to support the population. In other words the optimum population density in summer must always tend to be higher than that for the winter. In this way starvation, leading to lowered resistance and disease, the latter stimulated by overcrowding itself, may co-operate in reducing the population in the winter. Weather conditions will also affect the action of the other factors.

(*f*) *Restocking*. From what has been said above, we are forced to conclude that fluctuations among crayfish do occur, although we may accept or not the explanation of how they take place. At any rate, we have to explain how the main streams become restocked after an epidemic. Whenever crayfish are at all common some are sure to find their way into the smaller side streams and ditches, and the writer has found crayfish in the side streams of the Ock at the time the epidemic occurred in 1928. They still persisted in these streams in the following year when there were no crayfish in the Ock, and they still survive there at the present time (1933), although the main stream has not

yet become greatly replenished. Presumably it is from these side streams that the main water becomes restocked. Also the writer knows of several cases of individuals introducing crayfish from other rivers.

V. EFFECTS OF CRAYFISH EPIDEMICS ON OTHER ANIMALS.

The question naturally arises of whether fish and other freshwater animals are affected by the epidemics which occur on such a large scale among crayfish. But even if other animals were affected, it is extremely unlikely that the fact would have been observed, unless in the case of fish. The evidence about fish is somewhat conflicting but is given in full in the Appendix to this paper. The writer is of the opinion that fish, and especially perch (*Perca fluviatilis*), have decreased very largely of late years, but he is unable to find much evidence of fluctuations in their numbers; it must be borne in mind that such evidence would be difficult to obtain, as, unlike other sportsmen, few anglers appear to keep records of their bags. The figures of angling societies refer only to competitions which are held from time to time and under varying conditions, and are thus of little use. The parasite, *B. pestis astaci*, is known to attack freshwater fish of several species.

VI. SUMMARY.

1. Field observations and enquiry have shown the existence of large fluctuations in the numbers of crayfish (*P. pallipes*) in the Rivers Ock, Thame and Windrush, in the south of England. The fluctuations have taken place since at least 1885, and usually at about 13 to 14-year intervals.

2. The cause of these fluctuations is not known, but evidence points to disease (interacting with other factors such as climate, food supply and enemies) as the main agency.

3. The organism responsible for these epidemics in crayfish in England is not known, but may turn out to be *T. contejeani* or *B. pestis astaci*, both responsible for considerable epidemics on the continent of Europe.

4. It is pointed out that the periodicity in numbers offers an opportunity for foreshadowing the epidemics, and thus studying them intensively. In 1930 crayfish were scarce in the Ock after sudden disappearance in 1928; still abundant in the Thame and the Windrush where epidemics are to be expected during the present period.

5. Similar mortality occurs in river fish, but there are not enough data yet to connect this with crayfish cycles.

6. Repopulation takes places from side streams in which a few crayfish usually survive the epidemic; also by restocking through human agency.

APPENDIX.

EPIDEMICS AMONG COARSE FISH.

River Ock.

1880–1900 approx. Marcham and several miles up and down stream. Such coarse fish as roach, dace, chub, and perch were abundant in the Ock and especially in the smaller tributaries about 1880. They gradually dwindled from 1900 until now (1930); and at present all fish in the Ock are extremely scarce. This is attributed to the discontinuance of the practice of emptying sewage, on which the fish are supposed to feed, into the river and side streams. (C. J. Duffield, Marcham.)

1885. Cutts Mill, Abingdon, to "Noah's Ark," Marcham. Coarse fish died out about this time from a fungus disease. They have not returned in abundance since, although chub are fairly plentiful; perch are especially scarce. (C. C. Cheer, Cutts Mill, Abingdon.)

1886. Marcham to Stanford-in-the-Vale. Fish were not affected by crayfish epidemics at this time. (Dandridge, E. Hanney, and W. West, Marcham Mill.)

The numbers of coarse fish in the Ock have steadily declined since the beginning of the present century, although there is only one record of disease. But the chub, notoriously a hardy fish, has held its ground, while perch are very scarce. Of recent years no fish disease has been recorded in the Ock. The fungus epidemic of 1885 was about the time of the first crayfish epidemic in the Ock, but two observers deny that crayfish and coarse fish were affected at the same time.

River Windrush.

1915. Witney to New Bridge. In this year fish of all sorts were seen floating down the river. Cause of death unknown. (G. Holtom, Ducklington Mills.)

1930. Burford and district. Coarse fish are at present very plentiful in the Windrush.
(The Landlord, "Fox Inn," Burford.)

Fish appear to be plentiful in the Windrush at present, but this may be due to the fact that they are preserved in most parts of the river. There is only one record of an epidemic occurring in this river.

River Thame.

1889. Whole river. Simultaneously with the epidemic of crayfish there occurred an epidemic among coarse fish. The fish showed "a virulent ulcer or cancer on the side of the belly." They have not returned in much abundance since. (E. L. Franklin, Brookhampton, near Oxford.)

1914. Shabbington and district. Coarse fish have steadily become scarcer from about this date. No record of a sudden epidemic, nor do the observers believe the decrease to be connected with crayfish epidemics. (Two fishermen at Ickford.)

It appears that in the Thame, as in the Ock, fish are scarce compared to their abundance in the last century. There does not seem to be sufficient evidence to connect the epidemic of fish with that of crayfish, although the matter cannot be considered as by any means settled. Further evidence is badly needed before any speculations in this direction can be at all profitable.

River Thames.

A mortality of fish (pike, roach, chub, dace, and smaller fish) occurred in the Thames at Eynsham in July, 1929, and is given here as an example of pollution, which in this case was probably the cause of the mortality. At the time of the occurrence fish could be seen floating down the river in great numbers, indeed so numerous were they that they were raked out and burnt in large heaps in order to avoid contamination to the Oxford water supply. In reply to a question in the House of Commons, the Minister of Agriculture and Fisheries gave the following official statement: "A ditch of foul matter [water ?] was inadvertently discharged, owing to the lifting of a sluice by some unauthorised person, into the river, and this poisoned the fish."; The Thames Conservancy states that the "foul matter" was probably a more or less putrid liquid, contaminated with the decomposition products of decaying and fermenting vegetable matter. No search for bacteria or protozoa was made.

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A STATISTICAL ANALYSIS OF THE CLIMATIC FACTORS INFLUENCING THE DENSITY OF TSETSE FLIES, *GLOSSINA MORSITANS* WESTW.

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(*With Plates VI, VII.*)

I. Introduction.

From 1928 until 1932 the writer made a study of the fluctuations in the numbers of tsetse in relation to the seasonal variations in climate. An index of the seasonal fluctuations in the density of tsetse within the fly belt was obtained by means of "fly-rounds," which may be defined as surveys of tsetse numbers over a fixed route, repeated at definite short intervals throughout the year. By means of three such fly-rounds, 26 linear miles of fly belt provided samples of the density of tsetse at various seasons throughout $4\frac{1}{2}$ consecutive years. These fly-rounds were planned to tap the main vegetation communities, and consequently gave data that may be taken as representative of the fly belt as a whole.

Samples of the density of the tsetse were taken six times in every 5 weeks; two catchers followed the fly-round paths, stopping every 20 yards to collect all the fly that came to them. Sampling was not undertaken more often lest the objection be raised that the catching seriously depleted the tsetse population. For a detailed account of the method, and the precautions taken to insure the utmost accuracy, the reader is referred to Nash (1930, 1933).

The climatic factors were measured by means of instruments kept 4 ft. above the ground in a meteorological plot situated within the fly belt. Grass was allowed to grow up around the instruments, and at the time of the annual bush fires this grass was also burnt; hence the readings gave a measurement of the meteorological conditions experienced by tsetse at various times of year. A bi-metallic coil recording thermo-hygrograph gave dry and wet bulb readings from which the mean monthly temperature and saturation deficit were obtained. The instrument was housed in a Stevenson screen and was constantly set by the standard dry and wet bulb thermometer readings. Evaporation was measured by means of a Livingston-thone, white spherical, cup atmometer which gave excellent results. Rainfall was also recorded.

There is no difficulty in measuring the fluctuations in the factors governing

climate, but the measurement of the fluctuations in insect numbers is a much harder problem. The purpose of this paper is to show that fly data, obtained by the simple method described, are capable of yielding a relatively high degree of correlation with the meteorological data obtained from sources of recognised accuracy. The simple expedient of plotting the monthly means of each meteorological factor against the monthly means for tsetse shows with which factors a relationship exists (Nash, 1933); but this method falls short in that one cannot compare the relative importance of the rival climatic factors by a purely pictorial method. It is essential to measure the degree of correlation between fly and each climatic factor, in order to determine the relative importance of each, as well as to establish the nature of the lag between a change in a climatic factor and the resultant change in fly numbers. This can be achieved by calculating the coefficients of correlation existing between the fly figures and the figures for each component of the climate.

During the period under investigation, there was unfortunately one year of most abnormal rainfall, when the whole country was inundated by floods. The meteorological returns diverged widely from the previous means, and the fly population was in danger of extermination; it took over $1\frac{1}{2}$ years for the tsetse population to recover from this calamity and to return to a normal density. It seemed probable that the inclusion of the data from this abnormal period would upset the calculation of the coefficients of correlation; however it was decided to take the risk, and use the data for the full course of the investigation.

II. THE STATISTICAL INVESTIGATION.

The fly figures for this investigation have been taken from the fly-round which yielded the largest number of tsetse; over 120,000 tsetse were taken on this round during $4\frac{1}{4}$ years. Another reason for selecting this particular fly-round was its freedom from large game movements. It is very important to choose an area that supports a non-migratory food supply, as the movements of great herds of antelope can mask the effects of adverse season. For example, if the fly-round route encircles an area containing abundant, permanent water, great herds of game are certain to arrive from all directions at the end of the long dry season, bringing tsetse with them. Thus an appearance of increased fly density is produced, not because of an increased emergence of tsetse owing to favourable season, but because they have been carried into the area by converging herds of game. If the effect of season is to be studied, it is essential to obtain data from an area in which the possibility of such misleading results can be eliminated.

The tsetse data for this fly-round have been arranged in the form of monthly means, i.e. the mean of the four or five samples taken each month. Owing to daily fluctuations in fly *activity*, the average from a month's samples is regarded as a more reliable index of fly *density* than that given by any one

Photo. T. A. M. Nash

Phot. 1. Typical *Brachystegia microphylla* woodland. True habitat of tsetse fly (*Glossina morsitans*).

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sample taken alone. The coefficients of correlation have been worked out for the mean monthly fly figures combined with the mean monthly figures for temperature, rainfall, evaporation and saturation deficiency. In the case of each of the four climatic factors the fly density has been correlated with the meteorological reading for the same month, previous month, and for 2 months previous. Table I gives the coefficients of correlation for grouped data.

Since many entomologists have never attempted statistical work, it may be as well to quote an explanatory paragraph from *An Introduction to Medical Statistics* by H. M. Woods and W. T. Russell: "The coefficient of correlation may take any value between 0, which is the result when there is no relationship at all between the variables, and +1 or −1. When either +1 or −1 is the coefficient, it means that the correlation is perfect....A positive correlation means that as one variable increases in value the other variable also increases. A negative correlation means that as one variable increases the other decreases." The coefficient of correlation measures the linear or straight line relationship between variables. Having obtained the coefficients of correlation from grouped data one should then find the "correlation ratio"; the correlation ratio measures the amount of curvature in the data. If this ratio be considerably greater than the corresponding coefficient of correlation, it means that the relationship is "skew" or not linear. Attempts were made to calculate the correlation ratios on the data used in Table I. This method would have been ideal because it is known from previous work that there is a tendency towards curvilinearity, but unfortunately the readings were not sufficiently numerous to show trustworthy results.

Returning to Table I, it will be seen that the probable error is given immediately after each coefficient of correlation. As a conventional measure of the significance of the correlation, i.e. that the result is greater than might be due to chance, it is usual to regard a coefficient which is more than three times its probable error as being statistically significant.

Table I.

Nature of correlation	Month	Coefficient of correlation	Probable error	Period in months
Temperature and tsetse	Same	−0·199	±0·11	38
	Previous	−0·048	±0·11	37
	2 months previous	+0·305	±0·10	36
Rainfall and tsetse	Same	+0·190	±0·09	47
	Previous	+0·239	±0·09	46
	2 months previous	+0·185	±0·10	45
Evaporation and tsetse	Same	−0·487	±0·08	38
	Previous	−0·424	±0·09	37
	2 months previous	−0·196	±0·07	36
Saturation deficit and tsetse	Same	−0·794	±0·05	22
	Previous	−0·497	±0·11	21
	2 months previous	−0·216	±0·14	20

It will be seen that there is no correlation between tsetse and *temperature*,

in the same or previous months, but that with temperature of 2 months previous there is a very small but just significant association. There is no significant correlation between tsetse and *rainfall*, though the coefficients are uniformly positive. One suspects that the inclusion of the data from the year of abnormal rainfall may have seriously influenced the correlation in this case. Between the tsetse fly density of 1 month and the *evaporation* of the same and previous month there is clearly a significant association. In the case of *saturation deficiency*, it was only possible to use data relating to the last 2 years of the investigation, and consequently the year of abnormal rainfall, when the country was inundated by unprecedented floods, was not included; this suggests the possibility that the large degree of correlation between saturation deficiency and tsetse may be in part due to the exclusion of the abnormal year, with its freak meteorological returns, and that should that year have been left out in the other cases, high correlations might have also been obtained.

An attempt has been made to find the association of each climatic factor with tsetse by excluding the abnormal year. This has been done by making the period constant in every case, the last 22 months having been selected. Coefficients of correlation have been worked out using ungrouped data; the excellent results obtained are given in Table II. As the samples dealt with here are small, the usual test of significance does not apply. Fisher's (1930) table of values of the correlation coefficients for different levels of significance, in small samples, shows that in a sample of nineteen a correlation of 0·46 would be expected once in twenty trials. Any correlation of 0·46 or more has been regarded as statistically significant.

Table II.

Nature of correlation	Month	Coefficient of correlation	Period in months
Temperature and tsetse	Same	−0·192	22
	Previous	+0·056	21
	2 months previous	+0·331	20
Rainfall and tsetse	Same	+0·591	22
	Previous	+0·618	21
	2 months previous	+0·575	20
	3 months previous	+0·343	19
Evaporation and tsetse	Same	−0·729	22
	Previous	−0·569	21
	2 months previous	−0·255	20
Saturation deficit and tsetse	Same	−0·794	22
	Previous	−0·497	21
	2 months previous	−0·216	20

Temperature. No correlation is found between the mean monthly fly density and the mean monthly temperature.

Rainfall. The fly density of the present month is significantly correlated with the current rainfall, as well as with that of 2 months before. The long duration of the correlation is noteworthy. Further, since the coefficients are

Phot. 2. The black, ash-strewn country after the fires, which destroy the breeding grounds of tsetse fly (*Glossina morsitans*).

Photo. T. A. M. Nash

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positive, the following deductions may be made: the rains break, and as they continue in intensity so the fly density increases; then the rains end, and the lower the rainfall the fewer the tsetse, until at the end of the long dry season, when there is no rain at all, the tsetse are at their scarcest. These conclusions confirm those already reached (Nash, 1933), but in addition the results show that the duration of the lag is such that the rainfall of several months before influences the present fly density.

Evaporation. A high degree of correlation is found between the fly density and evaporation of the same month, as well as with the evaporation of the previous month. The lag is much shorter than with fly and rainfall. The correlation is negative, which means that as the evaporation rises the fly density falls, and that as the evaporation falls the fly density rises. This is consistent with the findings for rainfall. As the evaporation rises throughout the long dry season the tsetse become scarcer; then the rains break, evaporation falls, and fly density increases. It has been found by other methods that there is an optimum zone for fly in the evaporation range, and that occasionally the evaporation *falls* considerably below this zone with the result that fly density also *falls*; when the evaporation rises towards this zone fly density also rises, so that on these rare occasions a positive correlation occurs (Nash, 1933).

Saturation deficit. A very high degree of correlation is found between the fly density and saturation deficiency of the same month, and quite a high coefficient is obtained with the saturation deficit of the previous month. Again the correlation is negative. As the saturation deficit rises throughout the long dry season, so fly density falls; the rains break, the saturation deficit falls, and the number of tsetse increases. (Here also an optimum zone is believed to exist, and for occasional short intervals the correlation is positive.)

The long duration of the correlation between rainfall and fly is interesting. It must first rain for some time before the evaporation and saturation deficiency start to drop appreciably, and it is only after this that the fly density will begin to increase. Conversely, it is some time after the rains have ended that the evaporation and saturation deficiency start to rise, owing to the drying up of the bush, and not until they have risen considerably will the number of tsetse begin to decrease. One of the most valuable results of this investigation is that temperature alone is not correlated with the increase or decrease of the tsetse. Temperature is only important in so much as it influences the evaporating power, or the saturation deficiency, of the atmosphere. The writer does not suggest that temperature is immaterial in the life history of the fly, since it is well known that the duration of the pupal period depends upon temperature, but he does suggest that temperature alone plays but little part in determining the seasonal variations in fly density. It is the combination of temperature and humidity, no matter whether in the form of evaporation

or saturation deficiency, that is of vital importance in controlling the numbers of tsetse.

It is suggested that the channel through which this combination affects the fly density is through its effects upon the adults' longevity. Should the combination be favourable to tsetse the adults presumably live longer, emergence of young fly continues, an aggregation of tsetse ensues, and consequently there is an increase in the numbers of fly in the bush. On the other hand, if the combination of temperature and humidity be unfavourable, the longevity of fly presumably decreases; the adults die young, before they have had time to produce many offspring; and a drop in the number of tsetse is the result. An interesting point is that if the mean monthly evaporation and saturation deficiency are plotted, the two curves follow each other closely. Again when each of these two factors is correlated with fly, the coefficients are very similar, and in each case are negative. At first sight it may appear strange that such an agreement exists, when it is realised that the thermo-hygrograph, from which the saturation deficiency data is obtained, is housed in a Stevenson screen and records dry and wet bulb readings, whereas the atmometer is exposed to the sun and measures the amount of evaporation from the surface of a porous cup of known dimensions. On further consideration it becomes obvious that each instrument is influenced by the same climatic factors—temperature and humidity—as well as by wind, which must affect both instruments as it will increase the evaporation from the wet bulb, causing a decrease in temperature, as well as increasing the evaporation from the atmometer bulb.

The fact that the relationship between evaporation and tsetse and saturation deficiency and tsetse is so similar merely confirms the point that it is the combination of temperature and humidity that controls the readings of both instruments, and consequently both sets of readings are similarly correlated with fly numbers. An attempt was made to discover more precisely what degree of lag, between evaporation and resultant fly numbers, would give the highest correlation. Accordingly coefficients were worked out by weeks for lags varying from 1 to 5 weeks. Though no significantly different results were obtained, there is some evidence to suggest that the correlation is greatest when the lag is a fortnight.

An attempt was made to eliminate seasonal "trend" by correlating deviations of each month from the monthly means of the whole experience. This method was unsatisfactory because no reliable index of normal seasonal prevalence could be obtained owing to the influence on the data of the one abnormal year. It was impossible to avoid the normal period by taking only the last 22 months, as then there would not have been enough readings to justify the employment of this method.

III. SUMMARY.

By the use of statistical methods it has been shown that the numbers of *Glossina morsitans* are influenced by the incidence of the rainfall, and to a greater extent by that combination of temperature, humidity and wind which is expressed either in the form of evaporation or saturation deficiency. Temperature by itself does not affect fly density.

IV. ACKNOWLEDGMENTS.

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ON THE TRUE DENSITY OF TSETSE FLIES

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I. INTRODUCTION.

It has been pointed out by Lloyd and Johnson (1927), Nash (1930), the writer (1930), and Potts (1931) that the numbers of tsetse flies obtained from catches in the field do not necessarily give a true idea of changes in the actual density of these insects. The numbers give a *density-activity* index, which is dependent on the actual density of the fly, the physical conditions of the environment determining whether the fly will be active at all, and the physiological condition of the fly itself which will determine whether or not it will show itself to the catchers. Apart from such considerations as these, no density-activity index can give any idea of absolute density of flies per unit area, since it is never practicable to catch at any one time all the flies contained in any area of infested country. However, it is important to know the true density of tsetse flies, if only to test theories about their seasonal and annual variations based on the density-activity index. This paper contains an account of some preliminary experiments directed to this end.

II. POSSIBLE METHODS OF FINDING THE TRUE DENSITY.

(a) *In a closed area.*

In any area which is isolated from the remainder of the fly-infested bush it is evident that some estimate of the total contained fly population can be obtained by marking a known number of flies and subsequently finding what proportion these form of the total population. If the delay between marking and recapturing be short, the change in the constitution of the population owing to birth and death of individual flies will not have had time to affect appreciably the estimate obtained. If the delay be long, the deaths of the marked flies and the emergences of new individuals will have lowered the proportion of marked to unmarked flies. Some delay, however, will be necessary, owing to the fact that, since flies do not feed daily, individuals met with and marked on any day will be either more or less likely than any other individuals to be encountered on the following day. To overcome this difficulty it is necessary to mark flies on several successive days amounting together to at least half the period which normally elapses from feed to feed. This method is also desirable as tending to allow more complete diffusion of the flies through the isolated area, and hence fewer errors in the sampling when the recapturing begins.

Since some delay between marking and recapturing is inevitable, and since the birth and death rates (rate of change of population) are unknown, the errors due to these causes must be assigned maximal and minimal possible values. The minimal value is not difficult to guess, because every female must be allowed sufficient time to give birth to at least two larvae if the race is to survive. As this is scarcely possible in less than a month, it can be stated that a month is the least possible mean length of life of the fly. The maximal mean length of life is less important, since the greater it is the less will be the error in the final estimate of the population reached by this means. The value of the total population can thus be estimated within limits determined by the rates of birth and death.

(b) *In an area not closed.*

In an area not isolated from the general fly-infested country surrounding it, the problem is complicated by the diffusion of flies out of and into the area, and it will be necessary to adopt a different technique. If flies be marked daily in any area it is evident that the number of living, marked flies in the area and around it will increase to a maximum at which it will thereafter remain constant, subject to the steadiness of the rates of birth and death. Let N be the number of flies marked per day, and r the number of flies per N flies dying per day. Let t be the number of days elapsing after the start (day 0) of the marking until the rate of recaptures reaches its maximal, constant value. Then

$$\frac{N}{r} = t + 1.$$

Thus $(t + 1)$ is equal to the length of life of the fly in days.

Since N is known, we can determine the value of the death rate, r, by finding t experimentally; hence we can estimate the number of marked flies living in and around the marking area at any time after day t. Samples are then taken along transects running through the site of marking and representing the diameters of an imaginary circle the circumference of which is considered to lie outside the range of diffusion of all but a negligible proportion of the marked flies.

Then from the equation

$$\frac{\text{Marked flies in sample}}{\text{Unmarked flies in sample}} = \frac{\text{Total marked flies in circle}}{\text{Total unmarked flies in circle}}$$

can be deduced the total population of flies contained in the circle of known diameter. In practice there are difficulties in obtaining accurately the value of t, and from an experiment carried out on these lines in 1931 no satisfactory result was obtained. The method is outlined here in case it may prove useful to other students of animal numbers.

III. Site and technique employed for experiment by method A.

Aerial reconnaissance with Mr B. D. Burtt, Botanist, Department of Tsetse Research, and Mr C. N. Francombe, Pilot, Survey Department, Tanganyika Territory, resulted in the discovery in 1931 of an ideal experimental site in the western portion of the great Itigi thicket of Central Tanganyika Territory. The thicket is scarcely penetrated by tsetse (*Glossina morsitans*), which inhabits the *Berlinia-Brachystegia* woodland and its drainage valleys distributed, in this area, in comparatively narrow bands around and between the great blocks of homogenous thicket. On the north-west corner of the great Beruda thicket, north of Kazikazi station on the Central Railway, is a remarkable tennis racquet-shaped indentation of fly-infested woodland of *Berlinia-Brachystegia* with the associated drainage valleys. The expanded inner end of the "racquet" communicates by a very narrow "handle" with the country outside the thicket, the minimum width of the "handle" being 200 yards. The country internal to this constriction has been photographed from the air, and is thus found to comprise an area of almost exactly $2\frac{1}{2}$ sq. miles.

As fly are not numerous in the "handle" of the "racquet" it can be taken that, for experimental purposes, only a negligible amount of diffusion to and fro can occur within a few days. It can be taken, therefore, that in this locality we are dealing with a self-contained fly community neither contributing to nor gaining from the general fly population outside. The distribution and behaviour of the fly within the "racquet" are otherwise exactly similar to those observed by the writer in similar country throughout Central Tanganyika. (During the progress of the experiments an attempt was made to block completely the "handle" of the "racquet," but some passage of flies was still taking place across the barrier when the experiments were concluded.) In June 1932 a preliminary experiment was carried out. Flies were marked and re-marked on five successive days on a definite and constant transect winding about in the "racquet" for a distance of 8 miles. It was found that flies tended to be recaptured in greater numbers on the first and second days after marking; and further that on the sixth day (that following the five successive marking days) recapturing along the transect produced a proportion of marked to unmarked flies twice as great as that obtained by recapturing away from the transect. In August, therefore, when the experiment was repeated, the technique was modified. Flies were marked, as in June, on days 1 to 5, but on day 6 they were not recaptured specifically along the transect where marking had taken place. On days 6, 7 and 9 recapturing was carried out by pairs of men, an arbitrarily defined portion of the "racquet" being assigned to every pair. From the flies brought in the marked-to-unmarked proportion was determined. Naturally the error due to emergence

and death of flies was somewhat greater than before, but, against this, diffusion was more complete and the complicating factor of the time elapsing since the flies had last fed was to a large extent eliminated.

IV. Results of experiments.

The numbers of females marked and recaptured were too small to use; the figures following refer to males only.

A. *The June experiment.*

Date	8th	9th	10th	11th	12th	Total
Total marked	94	131	140	83	55	503
Recaptured on transect on 13th, Marked		...	...	...	28
„ „ Total		...	...	...	82
Recaptured off transect on 13th, Marked		...	...	...	11
„ „ Total		...	...	...	66
Total catch on 13th, Marked ...	...	...	...	...	39
„ All flies ...	...	...	...	...	148

The recaptures on the marking transect on the day following the final marking thus formed approximately one-third of the total catch, while away from the transect the proportion was only one-sixth of the total. Clearly, diffusion through the area had not been complete. However, an estimate founded on the total catch for the 13th is probably fairly near the true value. The estimate will be

$$\frac{503 \times 148}{39} = 1909.$$

If the average length of life is as low as one month, this estimate will be corrected to about 1700, and the corrected estimates from flies taken respectively on and off the transects will be 1200 and 2700 approximately.

These estimates are of course of the total population of male flies contained in the area.

B. *The August experiment.*

Date of marking	24th	25th	26th	27th	28th	Total	Marked and un- marked killed
Total marked	62	59	73	101	83	378	
Recaptured 29th	13	13	12	34	26	98	319
„ 30th	8	6	10	7	8	39	265
„ 1st Sept.	0	7	3	10	5	25	136
Totals	21	26	25	51	39	162	720

The estimates of the population derived from these figures, not allowing for death and emergence, are, for the respective days of recapturing,

$$\frac{378 \times 319}{98} = 1231;$$

$$\frac{378 \times 265}{39} = 2568;$$

and

$$\frac{378 \times 136}{25} = 2056.$$

The total estimate for all days combined is

$$\frac{378 \times 720}{162} = 1680.$$

Allowing as in the June experiment for a length of life of only 1 month, the first three estimates may be corrected approximately to 1100, 2300 and 1700, respectively. Estimates derived from recaptures of flies grouped according to the days on which they were originally marked, corrected as above, are respectively 1700, 1400, 1800, 1300 and 1400. (The correction for death and emergence is made by calculating how many flies of every group marked would have died by the time of recapturing, supposing about 3 per cent. die per day, roughly 100 per cent. per month.)

V. Conclusions from experiments.

From the several estimates of the total population of male flies contained in the area, it is likely that the true value lies between 1500 and 2000. (It must be remembered that, as the length of life of flies is probably over a month, the corrected estimates are all a little low.) As there is reason to suppose that the sexes exist in nature in approximately equal numbers, the value for the total population is probably between 3000 and 4000 flies.

The mean catch of male flies on the transect in the August experiment (the month when fly activity is supposed to be optimal) was eighty-eight in 8 miles, or eleven per mile. The total population of both sexes is suggested to be from 3000 to 4000 per $2\frac{1}{2}$ sq. miles, or from 1200 to 1600 per sq. mile. Thus in this type of country at times of optimal fly activity it is likely that one male fly per mile of collecting corresponds roughly to from 100 to 150 flies of both sexes per sq. mile, actual density.

These results, although inaccurate, form some advance on previous knowledge of the subject, and it may be hoped that other workers may be stimulated by them to devise more accurate means of estimating the actual density of tsetse-flies and other animals in their natural environment.

VI. Summary.

After consideration of the difficulties attending the formulation of any estimate of the density of tsetse flies in terms of number of flies per unit area of infested country, and of the importance of finding such an estimate, two possible methods are outlined. One is suitable for areas not isolated from the remainder of the fly-belt, but is attended by great practical difficulties; the other is suited only to experimentation in isolated areas of moderate extent, and is the one adopted in an experiment carried out in Central Tanganyika Territory in 1932. Both depend in principle on releasing a known number of marked flies, computing the number still living on some date subsequent to

their release, and finding what proportion in random samples taken on that date is borne by marked to unmarked individuals. The results of the experiment are expressed as the number of flies per sq. mile, actual density, corresponding to one male fly per mile, apparent density, collected by routine methods at the time of year when apparent fly density is at its maximum. The results of one experiment by the second method gave 1200–1600 flies per sq. mile.

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THE NATURAL CONTROL OF THE CABBAGE CATERPILLARS, *PIERIS* SPP.

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(*With two Figures in the Text.*)

CONTENTS.

I. INTRODUCTION.

IN the year 1930, the Lesser Cabbage White (*Pieris rapae* L.), a pest of European origin now widely distributed throughout the world, and considered by Comstock (*Manual*, p. 746) to be, in North America, the most injurious to agriculture of all butterflies, was discovered, for the first time, in New Zealand, in the environs of Napier in the North Island. In 1930, 1931 and 1932 the

insect increased enormously (Muggeridge, **10**) in numbers in the Napier-Hastings area and spread rapidly, extending its range to points at least 130 miles from the initial centre of infestation, and penetrating—probably through human agencies—even to Timeru in the South Island. It has already proved very destructive to cabbages and has also been found to attack both rape and chou moellier.

Early in 1931, the New Zealand Government therefore applied to the Imperial Institute of Entomology for a supply of the parasites of *Pieris rapae*. During the course of the work of collection the writer has had occasion to gather some facts, not noted by previous workers, which appear to throw some light on the problem of the natural control of lepidopterous pests in general, and of the Cabbage Caterpillar in particular. The following paper comprises a brief summary of these observations, together with an account of the practical work undertaken.

II. PRACTICAL WORK.

(a) *Choice of parasites and hosts.*

Many insect parasites, both dipterous and hymenopterous, have been bred from the various species of *Pieris*; but the most common and efficient of these appear to be the Braconid, *Apanteles glomeratus* L., attacking the larvae, and the Chalcid, *Pteromalus puparum* L., attacking the pupae. Initial efforts have therefore been devoted to the provision of sufficient supplies of these two species. In work of this type the usual procedure is to obtain the parasites it is desired to introduce from hosts belonging to the imported species, even though closely allied hosts, attacked by the same parasites, are present; for several recent authors have suggested that the ovipositing adults show a preference for hosts of the same species in which they have passed through the larval period.

In the present instance, however, this method was abandoned, owing to the difficulty of obtaining sufficient numbers of *P. rapae*. The female of this species deposits its eggs singly, on the outer leaves of the cabbage, and the young larvae, on hatching, bore through to the midribs of the inner leaves, making detection and collection very difficult without serious injury to the plant. *P. brassicae*, on the other hand, deposits its eggs in large clusters; the young caterpillars do not bore through the heart of the cabbage, but begin feeding on the outer leaves. The larvae of *P. brassicae* are thus much easier to collect than those of *P. rapae*. The maximum number of specimens of the latter species obtained from a single cabbage was 7, while 180 young larvae of *P. brassicae* were found on 2 sq. in. of leaf, and 3000 collected, on one occasion, from a group of 27 cabbages. *Apanteles glomeratus* appears to attack *P. rapae* and *P. brassicae* with equal facility. Most of the material exported to New Zealand was, therefore, obtained from the latter of the two species, though *P. rapae* was collected whenever this was possible. Caterpillars

of the first generation were not found anywhere in large numbers. About the beginning of August, 1932, only a few *P. rapae* and no *P. brassicae* were present. As the season advanced, the numbers of *P. rapae* gradually increased, but it was not until the first week in September that *P. brassicae* occurred in abundance.

(b) *Collection and rearing work for* Apanteles glomeratus *L.*

Since the Cabbage Caterpillars are very generally distributed throughout England, scouting was limited to the country surrounding Farnham Royal, and eventually a rather heavy infestation was discovered in the adjacent village of Burnham, where practically all the material shipped in 1932–3 was collected. All the caterpillars obtained were collected by hand. As they are very active, it was necessary to use a special collecting tin, in the form of a deep zinc pail, fitted at the open end with a detachable funnel. Caterpillars dropped into the funnel were unable to escape, but to ensure the safe transport of the material over long distances, a lid with a gauze covered opening was also provided. Generally speaking, small patches of cabbages in private gardens were the most fruitful collecting grounds. Small allotments, lying side by side, were somewhat less infested, while large fields were practically free from attack. The significance of these facts will be discussed later in this paper. On arrival at the laboratory the caterpillars were counted, those of *P. rapae* separated from those of *P. brassicae*, and were placed in shallow wooden trays, 2 ft. square and 4 in. deep, provided with a closely fitting cover, consisting of a wooden frame closed with a sheet of fine-mesh copper gauze. These covered-in trays have proved in practice more satisfactory than the usual Fiske trays with tanglefoot barriers, and have practically the same advantages.

Approximately 10,000 caterpillars were collected during the summer of 1932. About 500 were placed in each tray, and the trays were kept in piles in an outdoor insectary with open sides, in which the day and night temperatures were very similar to those in shaded situations out-of-doors. When the caterpillars had finished feeding, they crawled to the undersides of the lids of the trays and spun the silken carpet on which they normally transform. The healthy specimens, and those containing the larvae of *Phryxe vulgaris*, then pupated. At approximately the same time, the full-grown larvae of *Apanteles glomeratus* emerged from the caterpillars attacked by this species. Every day the trays were examined, and all frass, decayed leaves, dead caterpillars, chrysalids, and *Apanteles* cocoons removed, and numbers of hosts and parasites noted. The cocoons of *Apanteles glomeratus* are bound together very tightly in bundles which may contain as many as 80 individuals of the parasite. During the early stages of the work, while the daily emergence of parasites was small, it was possible to clean, separate, and count the cocoons, but this soon became a material impossibility, and it became necessary to devise a new method of estimating the numbers obtained.

The technique adopted was as follows: The masses of cocoons were divided into groups, comprising approximately 5000 specimens, and placed in open tins lined with double thickness of blotting paper. About 12 hours after, the refuse and debris, e.g. dead caterpillars, pupal mats, etc., were removed, and the cleaned cocoons placed in a dry room for 24 hours. By this process all excessive moisture, due to the bleeding of the caterpillars, was eliminated. By taking 4181 cocoons obtained from *P. brassicae* and *P. rapae*, and treated in this way, the average weight of 100 cocoons was determined to be 0·325 gm. From this constant the number of cocoons subsequently collected was calculated.

Immediately after they had been weighed and dried, the *Apanteles* cocoons were placed in cold storage at 32° F., and left there until the time for shipment arrived. They were then divided into masses of approximately 5000 specimens, and placed in glass-topped tins, lined with cotton-wool. These tins were placed with damp sphagnum moss in strong wooden boxes, measuring $12 \times 12 \times 10$ in., and despatched to New Zealand in the vegetable chill room of fast steamers, at a temperature of approximately 42° F. One consignment, comprising 2415 cocoons collected by Dr W. H. Thorpe, was despatched on December 16th, 1931; while three, prepared by the present writer, were sent in 1932: the first, containing 12,050 cocoons, on September 21st, 1932, the second, with 44,000 cocoons, on October 18th, 1932, and the third, with 44,049 cocoons, on November 15th, 1932. The 1931 shipment produced about 1200 adults, of which 60 were liberated in the field, while the survivors were used for breeding work under indoor conditions. News has just been received of the 1932 shipment, from which 29,671 *Apanteles* adults have already emerged, 28,570 being liberated in the field.

(c) *Collection and breeding work of* Pteromalus puparum L.

After it had been decided that *Pteromalus puparum* should be introduced into New Zealand, an attempt was made to make mass collections of the chrysalids of *P. rapae* and *P. brassicae* in the area in which the caterpillars had been gathered; but they proved to be exceedingly scarce and it soon became evident that a satisfactory supply could not be obtained in the field, and that it would be necessary to resort to breeding. A consignment of about 1600 healthy chrysalids of *P. brassicae* and 300 of *P. rapae* was therefore purchased from Mr L. W. Newman of Bexley, Kent, in order to supplement the supply obtained in the *Apanteles* work; and after a careful search in the Burnham district, 80 chrysalids of *rapae* and six of *brassicae* were obtained. These were placed in the incubator at about 80° F. and in 9–17 days two of the *rapae* and one of the *brassicae* produced adults of *Pteromalus puparum*. Two of these lots comprised both males and females, while the other was composed exclusively of females. These were mixed so as to permit of the fertilisation of all the females, and then divided into three communities each of which was

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placed in a small glass breeding jar, with a cotton-wool pad soaked in water, a raisin and a lump of sugar.

Five Pierid pupae were then placed in each glass. After about 12 hours the *Pteromalus* females began to oviposit and make feeding holes from which they drank the blood of the host. After 24 hours these pupae were removed and replaced by fresh specimens. The parasitised pupae were placed in the incubator at 80° F., until the adults emerged. These were then transferred to breeding cages and supplied with chrysalids; and this process was continued until a stock of about 500 adults had been obtained, after which the parasitised chrysalids were removed to an outdoor insectary, where the relatively low temperature induced a diapause. In this way 1685 parasitised chrysalids, 267 of *rapae* and 1418 of *brassicae*, were eventually obtained for shipment to New Zealand. The first lot of these, comprising 267 *rapae* and 409 *brassicae*, were packed individually in gelatin capsules (No. 000), perforated in order to allow of the escape of expired water vapour. These capsules were placed on sheets of corrugated paper, separated by double layers of cotton-wool, in tin boxes, which were packed in excelsior in stout wooden shipping boxes. In the second shipment, comprising 1009 pupae of *brassicae*, the gelatin capsules were omitted and the chrysalids placed directly in the furrows of the corrugated paper.

In both cases the consignments were despatched in the vegetable chill room of the vessels, at about 42° F. A report has just been received that both consignments arrived in good condition; the parasites were liberated and by the end of the season a parasitism of 40 % was obtained in the *P. rapae* around the district of liberation.

III. BIOLOGY AND INTERRELATIONS OF THE PARASITES.

During recent years a number of important papers on the parasites of *Pieris* have appeared: *Apanteles glomeratus*, in particular, has been the subject of a number of monographs. Only a few remarks concerning the species here treated will therefore be necessary.

(a) Apanteles glomeratus *L.*

Apanteles glomeratus L. is a very polyphagous parasite, and is recorded in the Parasite Catalogue of Farnham House Laboratory, from nearly 50 species of Lepidoptera. Gautier (4) maintains that it attacks *P. rapae* only when this happens to occur in close proximity to *P. brassicae*; and cites as evidence a field in which only 2 per cent. of the caterpillars of *rapae* were parasitised by *glomeratus*, as against 95 per cent. of the *brassicae* caterpillars. Our work lends no support to this view. It is true that 84 per cent. of the *brassicae* caterpillars collected produced *glomeratus* cocoons, while only 18 per cent. of the *rapae* caterpillars brought in were attacked by this species; but, as will appear later, this is probably due merely to the difference in habits of the two hosts. It is now generally admitted that this species oviposits in the small

larvae of *Pieris* and not in the egg. There is no evidence of polyembryony, but as many as a hundred larvae may develop within a single caterpillar. Caterpillars of *P. brassicae* produced, on the average, 44·7 cocoons of *Apanteles*; while those of *P. rapae* produced only 30. This difference is obviously correlated in the difference in size of the caterpillars of the two species. It would be interesting to know if the average number of eggs deposited in larvae of *brassicae* and *rapae* is the same, and, if so, when and how the supernumerary larvae are eliminated in the latter of the two hosts.

It is a curious fact that the larvae of the parasite normally emerge from the host after the latter has spun its pupal mat, and prepared for pupation. The spinning of the mat characterises the prepupal stage. One would therefore expect it to be closely correlated with the development of the imaginal rudiments, and with the accumulation of food reserves; and it would seem probable, also, that the development of the imaginal rudiments is dependent on an adequate supply of nutritive material. It is therefore interesting to note that, although in caterpillars from which parasites are about to emerge practically no fatty reserves are present in the adipose tissue, which is almost invisible in heavily parasitised specimens, the caterpillar is, nevertheless, able to produce the normal supply of silk and performs the actions that normally precede metamorphosis. These facts suggest that the development of the imaginal rudiments is scarcely, if at all, inhibited by the presence of the parasites, and that, in spite of their numbers, they interfere relatively little with the flow of nutriment to the more important organs and tissues of the body.

Another point of interest concerns the emergence of the parasite larva. As has already been noted, this occurs almost invariably after the host has spun its pupal mat. Why it should always occur at this time is not obvious. Though they are moderately uniform in size, the caterpillars of the host are not by any means identical, and probably do not provide a quantitatively identical food supply for the parasite colonies within them. Furthermore, the number of individual larvae in a parasite colony varies considerably: some caterpillars contain as many as 100 *Apanteles*; some as few as 20. Supposing that the media in which these groups are feeding are quantitatively identical, one would expect that the colony of 100 larvae would require much longer to reach the point where its numbers were ready to emerge, than the colony of 20 larvae. Nevertheless, they emerge, in fact, at about the same time; or, at all events, the moment of emergence seems to be determined by the behaviour of the host and not by the physiological condition of the parasite. It seems, therefore, that, under normal circumstances, the increase in the size of the parasite colony must produce a retardation in the development of the host of such a nature that, no matter how many parasites are present, the *Apanteles* larvae are practically always ready to emerge when the host has spun its pupal mat. The existence of such a physiological correlation is somewhat remarkable.

Nothing is known at present as to the stimulus that determines emergence. It seems, however, possible that, when the larva has reached a certain size, it becomes unable to subsist on the dissolved oxygen in the host's body fluids and must have direct access to the outside air. The writer hopes, at a later date, to investigate these problems in greater detail. It may be noted that there is a rough correlation between the daily temperatures and the emergence of the *Apanteles* exhibited in the accompanying graph.
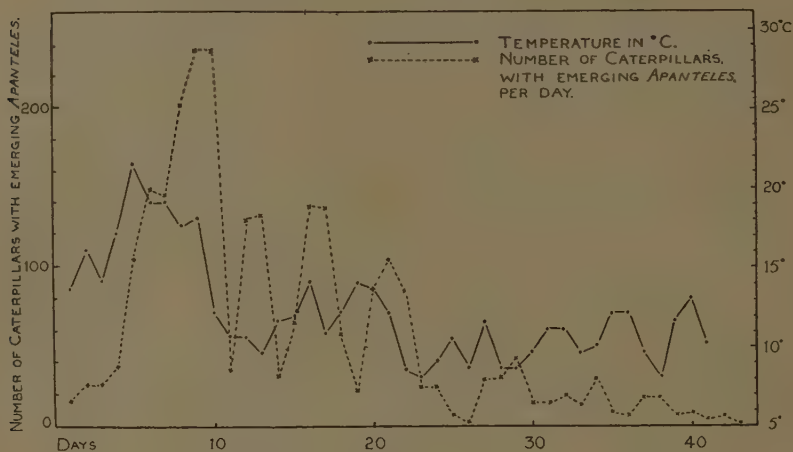

Fig. 1.

In 1932 the peak of emergence was on September 19th; at that time many young caterpillars were still present in the field and available for emerging parasites. Cocoons of this generation produced adults when kept indoors. It seems that exposure to low temperature determines a diapause, and that many, if not most individuals emerging in autumn actually hibernate. The onset of low temperatures at the time of emergence does not seem to have any ill-effect on the parasite larvae. To get information on this point, a group of larvae was placed in the refrigerator at 32° F., only 5 min. after emerging from the host. They spun their cocoons successfully and hibernated in the normal manner. Other cocoons were placed at 32° F., after the larvae had pupated[1], and left at this temperature for several weeks. Nevertheless, adults developed and issued normally, when the cocoons were transferred to higher temperatures.

On one occasion a mass of *Apanteles* larvae that had been soaked in heavy rain, while the larvae were spinning, was collected in the field. The larvae remained quiescent until the excess moisture had evaporated, and then

[1] The cocoons containing pupae are lighter in colour than those containing larvae, an effect due, apparently, to the contraction of the body of the parasite after the voiding of the meconium, which is visible as a black patch at the posterior end of the cocoon.

resumed spinning and completed their cocoons as usual with no more casualties than normally occur.

Parasites of Apanteles glomeratus *L.*

In February, 1933, masses of *Apanteles* cocoons were collected from fences and sheds in the gardens from which caterpillars had been obtained the previous autumn. These masses were divided up into small lots and placed in the incubator. From them were obtained the following parasites: *Hemiteles fulvipes* Grav., *Hemiteles areator* Panz., *Mesochorus pectoralis* Ratz., and *Dibrachys boucheanus* Ratz. When it appeared certain that no more insects would emerge, every cocoon was dissected and examined to confirm the earlier observations. From 9·81 per cent. of the 1284 cocoons collected nothing emerged, most of the *Apanteles* having died in the larval stage; 46·26 per cent. produced *Apanteles glomeratus* adults. The hyperparasites accounted collectively for approximately 50 per cent. of the cocoons, the actual figures being: 37·69 per cent. parasitised by *Hemiteles fulvipes* Grav., 4·83 per cent. by Chalcids (*Dibrachys boucheanus* Ratz.), 0·93 per cent. parasitised by *Hemiteles areator* Panz. and 0·47 per cent. by *Mesochorus pectoralis* Ratz.

It is evident, however, that to obtain a true figure for the percentage parasitism, it would be necessary to collect many thousands of cocoons; thus, in the preliminary experiments in the previous autumn, *Hemiteles submarginatus* Bridg. and *Tetrastichus rapo* Wlk. were bred in significant numbers from *Apanteles* cocoons, and it will be seen from the data given that no *Hemiteles submarginatus* were obtained from the February collection, and that all the Chalcids, with one or two exceptions, were *Dibrachys boucheanus*. However, it seems evident that, in England, the efficiency of *Apanteles* as a controller of the Cabbage Butterflies is largely impaired by hyperparasites; should the *Apanteles* be successfully introduced into New Zealand without the attendant hyperparasites it is probable that the first generation of the Pierids will suffer more heavily than it appears to do in England.

(b) Apanteles rubecula *Marsh.*

This parasite was obtained from a large number of the larvae of *P. rapae* but was never reared from *brassicae*, and does not, so far as is known, attack that species. *Apanteles rubecula* resembles *A. glomeratus* in habit. It is, however, a solitary parasite, only one larva developing within the host caterpillar. The larva is generally larger than that of *A. glomeratus*, and emerges when the *rapae* caterpillar is almost half-grown.

(c) Phryxe vulgaris *Fall.*

This Tachinid, which is not mentioned by Picard (15) in his paper on the parasites of *Pieris*, and is cited by Faure (2) as a species so uncommon that he obtained only two specimens during the course of his work, occurred

fairly frequently in the material collected at Burnham. It is a viviparous species, and in all probability deposits young larvae in the young caterpillars of the host. The early stages closely resemble those of *Zenillia roseanae*, B.&B., a parasite of *Pyrausta nubilalis* Hubn. whose biology has been described by Thompson and Parker (**20**). The larva of *Phryxe vulgaris*, like that of *Zenillia roseanae*, emerges from the parasitised chrysalid of the host at about the same time as the normal butterfly issues.

(d) Pteromalus puparum *L.*

This Chalcid is an internal gregarious parasite of the chrysalid. The biology has been studied by Picard (**15**), and the early stages described by Parker (**14**). It attacks a number of the Rhopalocera and seems to be invariably a primary parasite. Picard (*loc. cit.*) has noted that the female of *Pteromalus puparum* takes up its position beside caterpillars that are about to pupate and waits there, sometimes for hours, until the chrysalid appears, when it is at once attacked. He considers that this is due to an inhibition of locomotion produced by the contact of the parasite with the silken pupal mat, and that contact with silk immobilises many insects.

In order to test this hypothesis, females of *Pteromalus puparum* were placed on pupal mats, from which the chrysalid had been removed. The parasites were not, however, immobilised but moved to and fro across the mat in a normal manner, and left it at frequent intervals without apparent difficulty. Furthermore, it is certain the presence of the mat is not necessary to induce attack; for all of the pupae on which *Pteromalus* was bred in our experiments had been removed from their silken carpets. The behaviour of *Pteromalus* in pupae of apparently similar histories, and in similar environments, varied a good deal. Of 203 pupae exposed to attack for about the same length of time, and kept in the incubator at about 80° F., only 55 produced *Pteromalus* adults. Of the remaining 148, 5 produced *Pieris* adults, 50 died of bacterial or fungus disease, and 13 produced *Phryxe vulgaris*, while in 49 chrysalids, the *Pteromalus* larvae, for some unknown reason, went into a diapause[1].

Not all of the *Pteromalus* adults coming to maturity actually emerged. From 14 chrysalids, all issued; from 20, less than 5 failed to do so; while from 21 less than 5 issued. In the field the adults may (Faure, **2**) continue to emerge for several days, or even a week; but in the laboratory all the healthy adults issue within 10–15 min., and those left behind perish. Dead larvae of the parasite may also be found in the chrysalid after the emergence of the host; their death is probably due to a shortage of food, as they are usually crowded into the ends of the chrysalids, with the remains of the uneaten host tissues.

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[1] The remaining 31 chrysalids were unparasitised, but hibernated, and would not have produced adult *Pieris* till next year.

(e) The interrelation of the parasites.

This complex question cannot be treated in detail at present. A few obvious points may, however, be noted. *Apanteles glomeratus*, *A. rubecula*, and *Phryxe vulgaris* apparently enter the host at about the same stage. If the first two species occur together, *Apanteles rubecula* is probably the survivor, since it emerges when the host is only half-grown, while *A. glomeratus* does not issue until the prepupal stage. It is not, however, certain that *rubecula* and *glomeratus* larvae can live together in the same individual caterpillar, nor have we at present any proof that the larvae of *rubecula* emerge from hosts also containing *glomeratus*, but on a few occasions young larvae of both species were observed together. The larva of *Phryxe vulgaris* has been found on several occasions in caterpillars containing *Apanteles glomeratus*, and evidently does not seriously interfere with the development of the latter. *Phryxe vulgaris* does not enter on its active feeding period until after the host has pupated; and, as both species of *Apanteles* emerge before that time, it appears that the Tachinid is unable to compete with them, since it must inevitably perish after they have emerged. *Pteromalus puparum* does not attack the host until the chrysalid has been formed: it cannot, therefore, enter into direct conflict with *Apanteles*. It probably oviposits occasionally in chrysalids already containing the larvae of *Phryxe vulgaris*: the usual result of such encounters is unknown, but *Phryxe* has issued from chrysalids exposed to the attack of *Pteromalus*.

It is obvious that reduction in the number of the hosts surviving to pupate produced by the parasites of the larvae may have an adverse effect on the *Pteromalus* population. The non-parasitic mortality among the hibernating chrysalids appears, however, to be normally very high, and it may be that, whether *Pteromalus puparum* is abundant or rare in the autumn, the number of Pierid chrysalids producing butterflies in spring will always be small. On the other hand, the fact that all of the parasites, excepting *Apanteles rubecula*, attack other Lepidoptera, makes them to some extent independent, for reproduction, of the supply of *P. brassicae* and *P. rapae*.

IV. The natural control of the cabbage caterpillars.

(a) Seasonal history of P. brassicae and P. rapae.

The adults of these two species emerge in spring and deposit their eggs either in large clusters (*P. brassicae*) or singly (*P. rapae*) on the outer leaves of the cabbage. Upon hatching, the larvae of *P. rapae* bore through into the heart of the cabbage, while those of *P. brassicae* remain feeding on the outside of the plant. The caterpillars feed for almost a month after hatching. The adults of this brood appear in July and August, and give rise to a second generation, which is, in general, more numerous and destructive than the first generation, although more heavily parasitised (K. Smith, Text Book, 1931).

In 1931 we found, at the beginning of August in the Burnham district, only a few caterpillars of *P. rapae* and none of *P. brassicae*; after this date, however, *P. rapae* gradually increased in numbers; but *P. brassicae* was not found in abundance until the first week in September, though, because of its feeding habits, it was easier to detect than *rapae*. It is probable that the two species here treated react differently to climatic factors, but no accurate comparative study of their behaviour seems to have been made.

(b) *Natural control.*

(i) *Definitions.*

By *natural control* we mean the maintenance of the population of a species, by the action of natural factors, at a certain numerical level, whether this level is below the point where financially measurable loss to crops is produced, or not. This condition can be defined in itself, or *absolutely*, while economic control can be defined only *relatively*, in terms of other values themselves variable from time to time and from place to place. Natural control is necessary and inevitable. No species can go on increasing in numbers indefinitely. Nevertheless, the means by which the growth of populations is arrested differ in the case of different species, and even in the case of the same species, under diverse environmental conditions; and only a careful statistical study will reveal them. From the inadequate investigations made in the present case no certain conclusions can be drawn. The results obtained are, however, suggestive and may serve as a working basis for further studies.

(ii) *Factors limiting oviposition.*

Heavy rain, abrupt falls in temperature, and insect-eating birds probably effect some reduction in the numbers of the adult butterflies emerging in spring; but no definite information in regard to their action is available. Some authors, like Picard (**15**), have suggested that isolated Crucifers, because of their isolation, naturally escape attack, while extensive groups of such plants exert a mass-attraction on the butterflies. The results of our investigations did not support this hypothesis. Large open fields of cabbage, occupying several acres, were scarcely, if at all, infested; small allotments lying side by side were slightly more heavily attacked; while kitchen gardens, containing only a few cabbages, were in some cases completely ravaged. It may be that this difference is due to the presence of suitable hibernating quarters, such as sheds or fences in or near the kitchen gardens, and the absence of such shelters in the large fields; but this can hardly explain the distribution of an insect capable of migrating many miles from its birthplace before it deposits its eggs. Musy (**11**) claims that certain plants, such as tomatoes, if planted among cabbage, act as a repellant to the Pierids and prevent them from entering the fields. It seems possible that the converse may also be true, and that the presence of certain flowers, upon which the butterflies can feed, in or near the cabbage patches, determines, or at least increases the severity of invasions.

In many cases a kitchen garden was found to be heavily infested, while its neighbour, on the other side of the boundary wall, was practically free from caterpillars. Again, the Burnham area in general was severely attacked, while other districts 7–10 miles away were almost undamaged. It is very difficult to suggest any reason for such differences. It seems probable that they are due to the purely temporary and contingent action of a complex group of factors, comparable to those that produce the succession of shower and sunshine in a small spot on a particular day; so that it may be true to say that these individual differences are the result of chance, and thus scientifically impossible to predict individually, even though the average condition for the whole region could be foretold.

(iii) *Factors limiting larval numbers.*

(1) *Climatic.* Large numbers of caterpillars in the first and second stages are drowned in the water that accumulates on the leaf surfaces, and between the bases of the leaves, in rainy weather; heavy rains also cause the caterpillars to migrate to the lower surface of the leaves, where they cling only with difficulty to the wet surface, so that many fall to the earth. Wet weather may thus exert a controlling effect, though it is probably equally injurious to the natural enemies, and particularly to the hymenopterous parasites.

(2) *Disease.* According to Jegen (1918), from 16 to 35 per cent. of the caterpillars may die under natural conditions of bacterial disease. Many caterpillars died in the trays from this disease, particularly after the rearing work had been continued for about 6 weeks. It is apparently infectious (cf. Paillot, **13**), and was probably more severe in the trays than it is in the field. Of the caterpillars of *brassicae*, 59·17 per cent. died of disease, and of *rapae*, 61·9 per cent. In considering the mortality attributed to this cause it must, however, be noted that the figure really includes all larvae not otherwise accounted for, such as those that escaped and those accidentally killed. It may be added that caterpillars containing *Apanteles* larvae sometimes succumbed to the disease.

(3) *Parasites.* In the districts covered by these investigations, the only parasites found to attack and emerge from the larvae of the host were *Apanteles glomeratus* and *A. rubecula*, of which the latter only attacks *P. rapae*, while the former attacks both *rapae* and *brassicae*. Of 857 collected caterpillars of *P. rapae*, whose fate was actually determined, and none of which died from disease, 106, or about 12·3 per cent., were killed by *Apanteles rubecula*, while 161, or 18·8 per cent., succumbed to the attack of *A. glomeratus*. Of 3026 caterpillars of *P. brassicae*, whose fate is known, and of which none died from disease, 2550, or 84·21 per cent., were killed by *Apanteles glomeratus*. The proportion of *brassicae* killed by *glomeratus* was thus much higher than that of *rapae* destroyed by *glomeratus* and *rubecula* together. The results of dissections agree with those of the rearing work: of 40 caterpillars of *brassicae*, 35 were

parasitised by *glomeratus*; of 49 caterpillars of *rapae*, 12 only were parasitised by *glomeratus* and *rubecula*. This difference is probably due to the protective feeding habit of *P. rapae*, already discussed.

Dissections showed that, in the early part of the season, the majority of the parasitised caterpillars of *P. rapae* were attacked by *glomeratus*; later the parasitism by this species fell off, but that of *rubecula* rose so that the proportion of parasitised specimens (30 per cent.) remained approximately constant. Toward the end of September, almost all the parasitised caterpillars contained a larva of *rubecula*. These two parasites are thus, to some extent, complementary, though their periods of oviposition evidently overlap, and it would perhaps be advantageous to introduce both of them into New Zealand. As already shown, the individuals of *glomeratus* and *rubecula* emerging toward the end of the season, under outdoor conditions, pass, after spinning their cocoons, into a diapause, from which they do not emerge until the spring; but the cocoons formed earlier in the year produce adults, which are often able to reproduce; for young caterpillars of the host occur in the field almost until the end of the autumn.

(iv) *Factors limiting the numbers of pupae.*

(1) *General.* The Pierids attacking cabbage pass the winter, for the most part, as chrysalids. These are usually formed in places sheltered from wind, rain and direct sunlight. Many were collected from the inside of wooden structures in the field, such as outhouses abutting on back gardens; others were found on brick walls beneath window sills, or under eaves, but none on trees, fences, or any small structures, even though these actually stood amongst the cabbage plants. On two occasions chrysalids were found on the middle of window panes, in a position that afforded no protection either from weather or natural enemies. The chrysalids are, of course, naked, and since they remain in a diapause for a period of from 5 to 7 months in many cases, and are usually more or less accessible to predators and parasites, the destructive effect of controlling factors probably attains a maximum during this phase of life history. No evidence of the effect of climatic conditions has so far been obtained, the majority of chrysalids destroyed being apparently killed by parasites and predators.

(2) *Parasites.* The Tachinid, *Phryxe vulgaris*, is, in a certain sense, a parasite of the pupa, since it completes its development and kills the host in this stage; but, as already shown, it attacks the latter in the early larval instars. The available data indicate that many *Phryxe* larvae succumb through the competition with *Apanteles glomeratus* and *A. rubecula*; but a small proportion survives. From 203 pupae of *P. brassicae* and *P. rapae*, placed in an incubator, 13 adults of *Phryxe vulgaris* were obtained, so that the effective percentage of parasitism by this species was approximately 6 per cent. This would not necessarily have been any higher if *Apanteles* had not been present; though a

larger number of individuals of the Tachinid would have survived, together with a larger number of caterpillars of the host. *Pteromalus puparum,* which is a true pupal parasite, was uncommon in the material collected. Only 3 of 86 chrysalids obtained in the Burnham district were parasitised by this species. Certain workers (e.g. Friederichs, **3**) have observed a parasitism of as much as 80 per cent. by *Pteromalus*; but, in general, it appears to be inversely proportional to that of *Apanteles glomeratus,* the efficiency of the parasite being apparently dependent on the abundance of the host.

(3) *Predators.* No direct evidence as to the identity and work of the predacious enemies of Pierid pupae has as yet been obtained. The available data indicate, however, that an enormous proportion of pupae is destroyed by predators and that these predators are birds. In order to obtain some information on the fate of hibernating specimens 148 pupae of *P. brassicae* were placed out-of-doors in cloth slings, prepared as follows: small pieces of linen, measuring 4 in. by 1 in., were taken, and four slits, $\frac{1}{2}$ in. in length, were made at right angles to the long axis. The ends of the pupae were placed under the two narrow bands thus formed. The tension of the cloth was sufficient to hold the pupa without crushing it when the "sling" was attached to a solid support. These pupae were then nailed up in their slings in situations in the field similar to those in which fresh pupae or pupating caterpillars had been observed. A map of the area was made and the position of each pupa marked on it, so that none might be overlooked. At the same time, the concealment afforded by each position—as judged by human standards—was noted. The various positions were classified, from this standpoint, in three categories; the first (O) comprising pupae exposed on surfaces, such as fences, walls, windows, and trees; the second (OO), pupae semi-concealed under window sills, eaves, etc.; and the third (OOO) pupae actually inside closed, or partially closed situations, such as outhouses.

The results of this experiment are shown in Table I:

Table I.

Concealment	No. of pupae	No. disappeared after 1 month	No. disappeared between 1st month and end of winter	No. left in spring
O	37	34	1	2
OO	97	49	37	11
OOO	14	2	0	12
Totals	148	85	38	25

Thus only 17 per cent. of the pupae survived up to the time when this article was written (February 15th). The majority did not disappear completely, but had been emptied of their contents while still in their slings. Generally, the holes in the side of the chrysalids were small and indicated destruction by tits rather than by sparrows. It seems, therefore, that birds play a very

important part in reducing the Pierid population below the point to which the insect parasites have brought it. The percentage of the existing population destroyed by birds and *Apanteles* is very similar, but the value of these two controlling agencies is not altogether equal. To begin with, the numbers and action of an insect parasite are easily affected by minor meteorological variations, when these occur at critical points in the life history, while the numbers of birds are less subject to such influences and remain relatively constant from year to year. Furthermore, while the ovipository habits of *Apanteles glomeratus*, and *a fortiori*, of *A. rubecula* are, after all, relatively specific, birds are able to subsist on a wide range of food materials and will be much less affected by the numerical fluctuations of any one of the species on which they prey.

It therefore appears that birds practically always account for a large proportion of the individuals surviving to hibernate after the insect parasites have completed their work. Furthermore, it is probable that the normal bird population is able and willing to devour a number of chrysalids considerably in excess of that available during the present season, and that the situation at the close of the present season would not have been appreciably serious even if *Apanteles* had destroyed only a small fraction of the Pierid caterpillars. Nevertheless, if the parasites were altogether absent, there would probably be a notable increase in the number of individuals of the host surviving to reproduce; and, after a few generations, this might well bring the population up to a level where the food material available for insectivorous birds greatly exceeded their powers of consumption; after which their value as controlling agents, not only in relation to the Pierids, but in relation to their insect food in general, would diminish to the vanishing point. In other words, though the action of birds is a valuable complement to that of parasitic insects, and may automatically prevent outbreaks due to a temporary diminution in the numbers of parasites, it probably cannot replace them completely, nor is there any reason to believe that it can cope with the conditions of devastating increase met with in serious outbreaks.

V. Pupal coloration in relation to birds.

The data presented in the preceding section suggest that situations that appear to the human observer to afford concealment, really do provide it. Pupae classified by the observer as fully exposed actually disappeared more rapidly than those classified as semi-exposed. It would be interesting to determine whether pupae resembling the background in coloration are destroyed less rapidly than those whose colour contrasts with the object to which they are attached. The writer hopes to make an experimental study of the question next season. In the meantime, it might be of interest to record observations having an indirect bearing on the matter.

Previous workers (e.g. Poulton, **16**) have maintained that the pupae of

the species here studied tend, within certain limits, to be homochromic with the background on which they are found; and have inferred that this conformity is protective. Now as has already been mentioned, the caterpillars reared for *Apanteles* were all confined in trays having a fine-meshed copper gauze lid. With a few exceptions, all the unparasitised specimens pupated on the underside of the lid, that is to say, on the copper gauze itself. The trays were stacked in shelves in such a way as to leave about 2 in. of space between the lid of one box and the bottom of that above it, so that only very diffuse light could enter.

The colour of the background in which the caterpillars pupated was therefore practically constant, consisting of a weak light, mingled with reddish reflections from the copper gauze. Since the background was uniform in colour, one would have expected to have obtained pupae of the same shade, homochromic with the substratum. The colours of a batch of 279 *P. rapae* pupae formed in the trays were, however, as follows:

Colour			Nos. of pupae
Pinkish	...	...	27
White ...	...	...	61
Very light brown	...	...	60
Dark brown	...	...	70
Dark green	...	...	40
Pale green	...	...	15
Emerald green	...	...	6
Total	...	...	279

Thus, instead of exhibiting uniformity in colour, or even a predominance of any particular shade, the pupae exposed on this particular background were of many different tones, which appear to lie along a curve of probability, with a tendency to brown at the maximum and pink and green at the two extremes. In other words, the distribution of colours in this experiment appears to be due to chance. Furthermore, the colour of pupae collected in the field often differs very markedly from that of the objects to which they are attached. For example, a pupa of *P. rapae*, found on dark red teak, was described by one observer as white, and by another as a very light brown. It could hardly have been more conspicuous against the background.

Experiments were performed by Poulton and Sanders in 1898 to find the degrees of protection afforded by the various shades (gold—dark brown) of *Vanessa urticae* pupae when exposed on different backgrounds. In the field the gold forms are usually found on nettles and the dark forms on trees, fences, etc. A study of the experiments shows that when the usual backgrounds were exchanged "some positive and some negative results" were obtained. This means that the birds did not take advantage of the increased conspicuousness of the pupae due to the reversal of the usual backgrounds. On the other hand, there was always a higher percentage of pupae eaten by birds when smooth surfaces, such as fences, were used as a background, than

when the pupae were semi-concealed in the nettles or by the rough bark of a tree; a result which is to be expected.

If birds have controlled the evolution of Lepidoptera to such a large extent as has been suggested in cases of mimicry, it is somewhat surprising to find the habit of pupating on exposed surfaces, such as fences and even windows, which is possessed by so many larvae, has not been eliminated by natural selection acting through predatory birds, for it would be expected that nearly all lepidopterous larvae would, by now, have the habit of pupating only in concealed places (which would appear easier to obtain than homochromic colours).

The writer therefore ventures to suggest that the pupae of the Pierids, at least, are not adequately protected by their coloration. Such protection as their habits give them is primarily due to their pupation in situations where they are definitely concealed from view, so that conformity with the background is of minor importance. As has been shown, the pupae normally differ a good deal in colour, and certain of them naturally chance to form on backgrounds of a somewhat similar shade. The writer is inclined to think that it is such coincidences that constitute the basis of the notion of protective coloration in this particular instance; and that its protective value in relation to the natural enemies of the insect is practically negligible.

In a contribution to a recent discussion on protective adaptations (**19**), Professor Poulton describes the results of attempts to rear the caterpillars of *Abraxas grossulariata* L. and *Amphidasys betularia* L., sleeved in muslin bags on the food plants. The aposematic caterpillars of *grossulariata* suffered very rarely, and then only from enemies accidentally enclosed with them. The procryptic caterpillars of *betularia* were, however, readily discovered by both birds and wasps, and so rapidly destroyed that eventually the attempt to breed them in the open had to be abandoned. Thus, although these larvae present an undeniable resemblance to twigs, enhanced by the habit of remaining immobile by day and, in the experiments cited, were at least partially concealed from view by the muslin sleeve, and in the later attempts by two sleeves, one within the other, their enemies had apparently no difficulty in finding them. The "protective adaptations" of the *betularia* larvae do not seem, in this instance, to have afforded them much protection.

When cases of this kind are brought forward, the supporters of the idea of protective adaptations commonly reply, in the first place, that no protection is absolute, and, in the second place, that as the prey, under the influence of natural selection, becomes more and more similar in appearance to the environment the senses of the predator become, *pari passu*, more acute, so that it remains about as capable of detecting its victim as it was at the beginning of the process. We thus arrive at the rather humorous conclusion that the alleged "protective adaptation" is not particularly protective at all; it is merely *intended to be protective*. But though it may be possible, in certain cases, to determine experimentally whether a particular form and coloration afford

protection, it is somewhat difficult to see how one could demonstrate scientifically that it is *intended* as a protection, though it does not, in fact, protect.

The "protectionists" are not unaware of this difficulty. They attempt to elude it by citing defensive structures used by men, such as armour on battleships, which we positively know to be protective, though they fail in many cases to fulfil their intended functions owing to the parallel development of weapons of offence. But the argument is fallacious. The case of an armoured battleship is one we can understand, because it has been explained to us by the designer; but we can have no such knowledge of the case of the procryptic caterpillar. Of the "intentions" of Nature we know nothing.

It is, of course, probable that a certain conformation or coloration may, in certain contingencies, preserve individuals that would otherwise have been destroyed. But since their utility is admittedly only relative, it seems unlikely that they play a sufficiently important part in the economy of the species to be preserved by natural selection; and it is still more difficult to believe that the minute differences in appearance from which, according to the selectionists, procryptic form and colour have been slowly built up, can have, in Nature, any definitely protective significance.

An ingenious attempt to side-step these difficulties has been made by Nicholson (**12**). This author considers that the agencies controlling the numbers of organisms may be divided into two classes: selective agencies, whose capacity for destruction depends upon the intrinsic characteristics of the organisms on which they act—on the degree of resemblance between the individual and the environment, for example; and non-selective agencies, whose capacity for destruction is practically independent of the intrinsic character of the organisms affected by them, but varies in intensity according to the number of these organisms, their destructive intensity increasing as the organisms become more abundant, and decreasing as they become rare. The selective agencies improve and build up "adaptations" such as mimetic resemblances; the non-selective agencies regulate numbers. To understand how the combination of these two groups of factors work, let us suppose that the adult stage is chiefly affected by selective factors, the younger stages by non-selective factors. The appearance of a "protective" resemblance will result in a decrease of the number eliminated by the selective factor. More individuals will survive to reproduce. The increase in the number of young stages will automatically cause an increase in the intensity of action of the non-selective factor. More individuals will thus be destroyed than in the time preceding the appearance of the "protective" resemblance. The appearance of a "mimetic" variation in the interior of a species will not therefore produce a permanent increase in the numbers of this species. The offspring of the mimetic strain will not, during the early stages, be any more protected than the offspring of the non-mimetic strain. Mimetic species will not be any more "successful"—taking abundance to be the measure of success—than non-

mimetic species. Mimetic species cannot therefore "have any advantage over non-mimetic species in their natural environment" (Nicholson, *op. cit.* p. 99). "Purpose" and "advantage" can have no place in the true explanation of mimetic resemblance" (*loc. cit.* p. 99). Mimetic resemblance "simply fits an insect more perfectly to its normal environment" (*loc. cit.* p. 98); but "neither the species nor the individual, on the average, enjoys any protection due to the possession of mimetic resemblance." In order to explain its production there is, therefore, "no need for any teleological concept of ultimate purpose."

By describing the mimetic resemblance as fitness to the environment and affirming, at the same time, that it confers no advantage either to the species or to the individual, Nicholson endeavours to have his cake and eat it. The fallacy of his argument is however obvious. If we say that mimetic resemblance can only be described as advantageous or purposeful, if it enables the species to increase in numbers, or improves the chance of survival of every individual of the mimetic type, even in stages of development when that individual is *not mimetic*, then we are entitled to say, on the basis of Nicholson's argument (supposing it to be otherwise valid), that the mimetic resemblance confers no advantage. But it would be just as reasonable to say that the fact that a man carries a fountain pen will not protect him from sunstroke, and that therefore we must not attach any teleological significance to fountain pens. It is evident that any advantage conferred by mimetic resemblance will be enjoyed only by the organism that possesses it, and in the stage in which it is possessed. If the chance of survival of the average mimetic individual, in the mimetic stage of its life history, is greater than that of the non-mimetic individual in the corresponding stage, then the possession of the mimetic resemblance is to that extent an advantage; and its advantageousness is in no way affected by the susceptibility of the individual to the action of destructive factors in other stages, unless there is an *intrinsic physiological* correlation between this susceptibility and the existence of the mimetic appearance. That the mimetic resemblance is in that degree advantageous, Nicholson himself is obliged to admit: that much is indeed necessary to explain the development of the resemblance. If mimetic resemblance has been produced by natural selection, it is quite proper to say that it confers an advantage; whether it is "purposeful" or not is another question, which we need not pursue at present.

It may be noted that, although Nicholson's suggestions are put forward to alleviate certain difficulties felt in connection with the theory of natural selection, they have not been enthusiastically received by students of mimicry. Professor Poulton (**18**) considers that an unnaturally sharp distinction has been made between the "eliminative" attacks of invertebrate enemies upon the early stages and the "selective" attacks of vertebrate enemies in the final stages. It seems, indeed, if we admit the premises of the theory of natural selection, that practically all destructive environmental factors might, in fact, exert a selective action in some way or other.

However this may be, the suggestions of Nicholson have no particular bearing on the objections put forward above. The question here raised is not whether mimetic resemblance confers a general advantage to species or individuals; but whether it confers the advantage it must confer if it is to arise under the influence of natural selection. Is it true that individuals resembling certain available backgrounds in the environment have, in nature, a greater chance of survival than individuals which do not resemble their backgrounds,
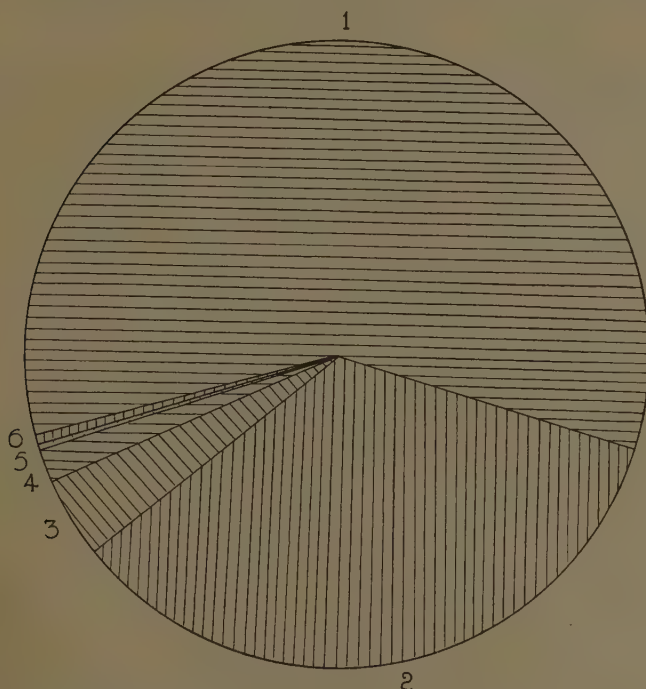

Fig. 2. Graphical illustration of the fate of the second generation of *Pieris brassicae* L. in England, 1932. 1. Disease of caterpillars. 2. Parasitised by *Apanteles glomeratus*. 3. Eaten by birds. 4. Disease of pupae. 5. Parasitised by *Pteromalus puparum*. 6. Emerged as adults.

or are less similar to them? The idea is no doubt plausible, but the evidence in support of it is not, at present, convincing. Certain selectionists now suggest that the increase in the chance of survival need only be very slight—for example, 0·1 per cent.—in order to determine the evolution of a mimetic form. But it is obvious to anyone who has attempted to carry out quantitative studies in the field, that the demonstration of such a very slight advantage in nature would be excessively difficult, if not impossible; and that the strain on the theory has been relieved only by making it almost unverifiable.

VI. Summary of the data on natural control.

We may now summarise the results of the preceding observations on the controlling factors of the Pierids. Supposing that at the beginning of the second generation we have in a field 10,000 young caterpillars of *P. brassicae*, the fate of these is as shown in Table II:

Table II.

Controlling factor	Destroyed %	No. of *Pieris* destroyed	No. of *Pieris* remaining
—	—	—	10,000
Disease of caterpillars	59·17	5917	4,083
Apanteles glomeratus	84·21	3438	645
Disease of pupae	27·00	174	471
*Pteromalus puparum**	3·00	14	457
Birds	93·00	425	32

* Figure based on the collection of only 86 pupae.

The mortality attributed to disease in Table II is probably much higher than that which normally occurs in the field; on the other hand, no account has been taken of the mortality of the eggs and young larvae, though it is probably considerable. Finally, the percentage of parasitism attributed to *Pteromalus puparum* is certainly low. Picard (**15**) affirms that, in the regions where his studies were made, very few chrysalids escape the combined efforts of *Pteromalus puparum* and *Pimpla instigator* F. To say that of 10,000 eggs, deposited at the beginning of the second generation, only 32 produce adults, of which, of course, only 16 are females, is therefore not to overestimate the combined effect of the factors of natural control. Were it not for these factors, among which the most important are the parasites and predators, the cultivation of cabbages, in regions where its Pierid enemies exist, would, as Picard points out, be an impossibility. The introduction of the insect enemies of *P. rapae* into New Zealand ought, therefore, to prove of real benefit in checking the ravages of the pest.

VII. Acknowledgments.

VIII. Summary.

1. In 1930, the Lesser Cabbage White was accidentally introduced into New Zealand, where it is now increasing in numbers and spreading rapidly. In the hope of arresting its spread, and diminishing the damage it causes, the

Government of New Zealand decided to import the parasites attacking it in Europe.

2. The present paper comprises an account of the methods used in the collection and shipment of the parasites of *Pieris*, together with observations on their biology and interrelation; with an attempt to evaluate the effects of the various factors involved in the natural control of the Cabbage Whites in the areas studied.

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RHYTHMIC ACTIVITY IN THE SHORT-TAILED VOLE, *MICROTUS*

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(*With two Figures in the Text.*)

I. INTRODUCTION.

THE original aim of this work was to ascertain whether voles are more active by day or by night and to study their rhythms under controlled conditions of light and feeding. It was found, however, that *Microtus* has a short 2- to 4-hour rhythm of feeding activity as well as a longer 24-hour rhythm with a maximum just after sunset and a higher average of activity at night. Richter (1927) correlates similar short-period activity of the Albino Rat with a hunger response brought about by regular stomach contractions. Johnson (1926) has shown that the American Forest Deer Mouse (*Peromyscus*) has a nocturnal rhythm which persists in total darkness but which can be reversed if the mice are kept in artificial light during the normal hours of darkness. Elton and others (1931, pp. 716–18) found that the Wood Mouse (*Apodemus sylvaticus*), in the laboratory, has a nocturnal rhythm apparently controlled by light with a bimodal periodicity during the night indicating the major feeding periods.

This work forms part of a 4-year scheme of research into the ecology of voles in Great Britain, which is being carried out with the aid of a grant made by the Royal Society to Mr Charles Elton, whom I wish to thank for much valuable help and advice. I am indebted to Prof. E. S. Goodrich, F.R.S., for allowing me the facilities of the Department of Zoology and Comparative Anatomy. Mr R. M. Ranson's knowledge of the care of voles and his attention to the experiments when I have been away have been invaluable.

II. METHODS AND MATERIAL.

To obtain records of the activity of a small mammal such as *Microtus* it is necessary to construct a cage that will relay the movements of the animal to a recording kymograph. Johnson (1926) had cages suspended from rubber bands; an indicator on the cage was in contact with a circular disc of smoked paper which was revolved by a modified alarm clock. Previous work at Oxford on the activity of *Apodemus* (Elton and others, 1931) was carried out by using a cage with a movable floor supported on springs; the indicator, attached to the floor, made contact with a drum of smoked paper which was

revolved once in 24 hours. The cages used in the experiments consist of two parts; a wooden framework, similar to an ordinary cage, with a small nest-box partitioned off from the feeding compartment, and two rectangular zinc trays that fit inside the compartments. These trays are suspended at the corners by rubber bands and move freely inside the cage under the weight of the mouse; this movement is recorded by indicators, one on each tray, which are in contact with smoked paper on a drum. This is revolved once in 24 hours by means of an ordinary clock fitted with a driving wheel that has twice the usual number of teeth. The drum is 24 in. in circumference so that 1 in. on a record equals 1 hour. The records are transcribed on to a large sheet of graph paper to the nearest 6 minutes, one unit therefore equalling one-tenth of an hour (Fig. 1). With this recording arrangement the records of nest-box and of feeding compartment activity act as a check on each other.

The cages were kept throughout the experiments in a hut with a skylight above them. There was no artificial heat.

The series of experiments selected here for analysis were carried out on one individual, a female vole, bred in the laboratory from stocks derived from North Wales and Scotland. There are two species of vole found on the mainland of Great Britain: *M. hirtus* being the southern and lowland species and *M. agrestis* the highland form. The voles in this and other series of experiments were probably *M. agrestis*, although it is not certain as the exact distribution of the two species has not yet been worked out.

The animals were fed by placing on top of the cages fresh grass to be pulled through the wire by the vole, while corn was placed inside. Water was supplied by the drop method. Table I describes the feeding conditions.

Table I. *Time of feeding and type of food given during the experiments.*

Exp.	Date	Time of feeding	Type of food
A	Oct. 23rd–Nov. 1st	5.0 p.m.	About 30 gm. fresh grass, corn and water
B	Nov. 2nd–Nov. 11th	12.0 noon	About 10 gm. fresh grass, hay, grass-seed, and water
C	Nov. 15th–Nov. 26th	5.0 p.m.	As Exp. B
D	Nov. 29th–Dec. 7th	10.0 a.m. and 5.0 p.m.	About 20 gm. fresh grass, hay, corn and water at 10.0 a.m. and about 20 gm. more fresh grass at 5.0 p.m.

The object of changing the time of feeding and the type of food was to find out whether these factors had any effect on the 24-hour rhythm; the "hay, grass-seed and a little grass" diet was given to see whether food that does not go stale would bring about a more even distribution of activity.

III. Results.

In Fig. 1 the records of activity are shown. The short 2- to 4-hour periodicity and the longer 24-hour rhythm can be clearly seen.
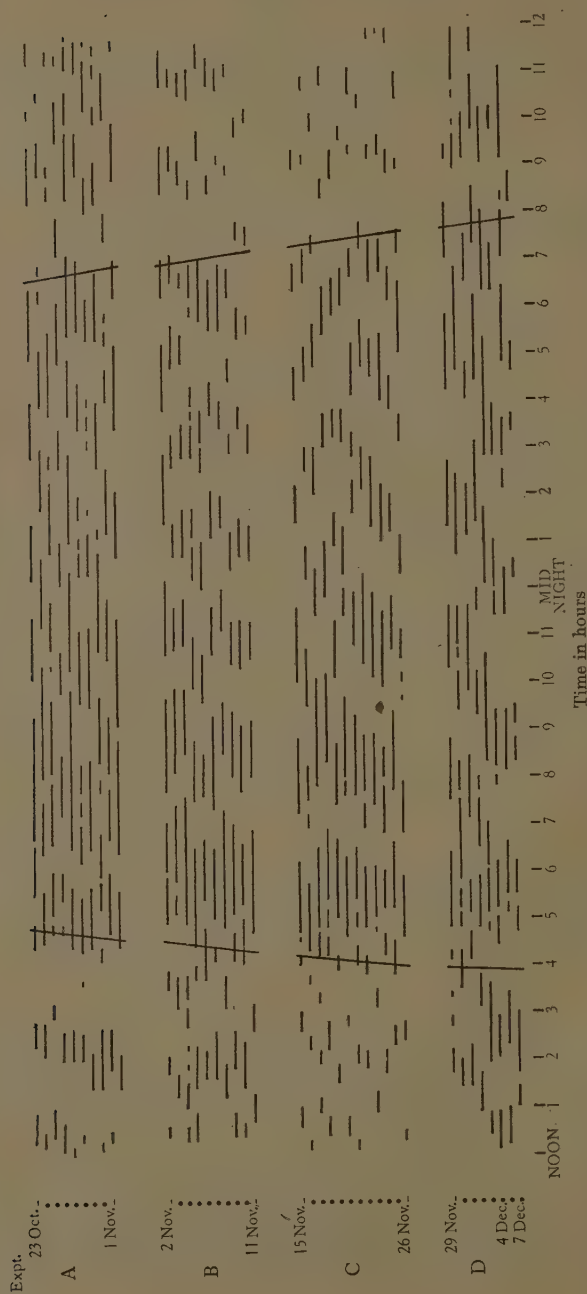
Fig. 1. Records of activity of the same vole in four experiments under different conditions of feeding (Table I) and gradually lengthening nights. Horizontal lines show periods of activity, sloping lines mark sunset and sunrise. The records show both the short 2- to 4-hour rhythm and the long 24-hour rhythm.

Since *Microtus* is herbivorous and feeds mainly on grasses it has to feed for a considerable part of the day in order to obtain enough food, because of the high water-content of grass. It has been found that a vole weighing 27 gm. eats about 16 gm. grass and nearly 3 gm. corn per day, or about 6 gm. of dry food. The grass contained 80 per cent. water, so that to obtain enough dry food on a diet of grass alone the vole would have to eat about 30 gm. per day; i.e. about its own weight. The bulk of the food that can be digested at one meal is limited by the size of the stomach; it is therefore reasonable to assume that the basis of the short rhythm is feeding, and that a vole has usually about ten meals a day. Each active period is followed by a resting period, during which there is no activity except small movements in the nest box and occasional excursions into the feeding compartment. It is during this time that the meal is digested. It seems likely that the onset of activity after the digestion of the previous meal is caused by a hunger reaction bringing about a feeling of restlessness which is satisfied by feeding (Richter, 1927). Until it is known how much of the active period is taken up with feeding it will be impossible to explain the longer active periods at night. It may be that there is a minimum time for filling the stomach approximating to the length of the short periods and that at night energy is dissipated in other activities such as sharpening the teeth, play, etc.

Table II. *The average length of activity in minutes per hour in four successive experiments. The figures were calculated from the original records (Fig. 1) of the one vole.*

| Experiment	A	B	C	D
	Oct. 23rd–Nov. 1st	Nov. 2nd–11th	Nov. 15th–26th	Nov. 29th–Dec. 7th
Time	(10 records)	(10 records)	(12 records)	(8 records)
12.0– 1.0 p.m.	17·4	13·2	10·0	16·5
1.0– 2.0	12·0	27·6	8·0	22·5
2.0– 3.0	29·4	18·0	16·0	32·2
3.0– 4.0	1·8	19·2	6·5	17·2
4.0– 5.0	27·0	24·0	28·5	22·5
5.0– 6.0	46·8	52·2	53·5	48·0
6.0– 7.0	32·4	49·2	22·5	28·5
7.0– 8.0	47·4	21·0	31·5	25·5
8.0– 9.0	45·0	49·2	44·0	33·0
9.0–10.0	35·4	27·6	20·5	28·0
10.0–11.0	41·4	28·2	33·0	23·2
11.0–12.0	33·0	28·8	32·5	25·5
12.0– 1.0 a.m.	32·4	22·8	19·5	22·5
1.0– 2.0	33·6	39·4	22·5	26·8
2.0– 3.0	25·2	15·0	20·5	24·8
3.0– 4.0	30·0	28·2	15·5	22·5
4.0– 5.0	32·4	16·2	24·0	30·0
5.0– 6.0	34·8	22·8	20·5	32·2
6.0– 7.0	28·2	32·4	26·5	24·8
7.0– 8.0	9·0	5·4	13·5	31·2
8.0– 9.0	25·8	12·6	5·5	12·0
9.0–10.0	24·0	13·2	13·5	33·0
10.0–11.0	21·6	16·2	10·5	18·0
11.0–12.0 noon	19·2	10·8	4·0	10·5
Average for 24 hours	28·5	24·7	20·9	25·9
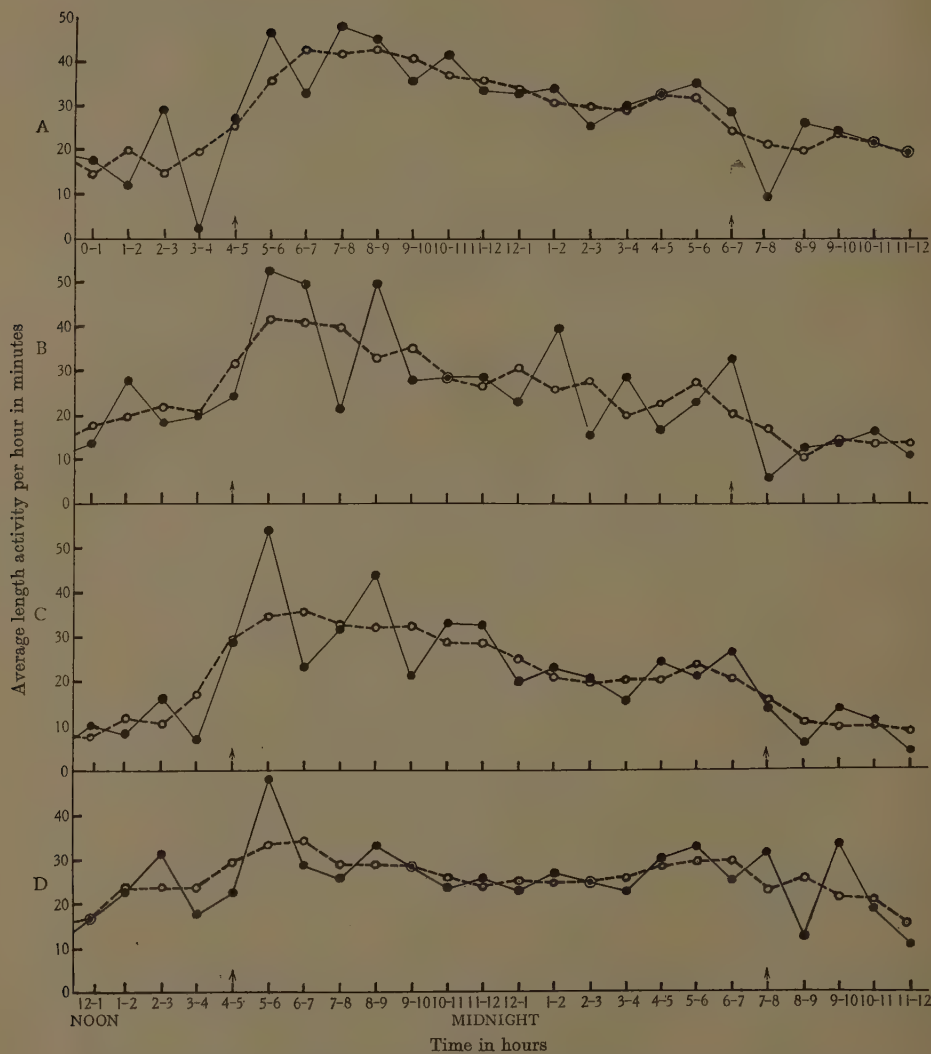
Fig. 2. The curves show the difference in activity between day and night (Table II). Continuous lines are average length of activity per hour, broken lines the smoothed averages. Times of sunset and sunrise are indicated.

Table III. *Comparison between the average activities by day and by night in four experiments.*

Exp. A

Date	Day Length activity in hours	Day Activity %	Night Length activity in hours	Night Activity %
Oct. 23rd	3·3	33	9·0	64
24th	2·3	23	8·6	61
25th	1·8	18	8·6	61
26th	3·1	31	7·1	51
27th	4·3	43	10·8	77
28th	3·0	30	7·6	54
29th	3·0	30	7·3	52
30th	3·6	36	8·3	59
31st	2·7	27	7·5	54
Nov. 1st	2·5	25	9·6	68
Average	2·96	29·6 (18–43)	8·44	60·1 (51–77)

Average % difference   **30·5**

Total average activity in 24 hours   11·4

% average activity in 24 hours   47·5

Exp. C

Date	Day Length activity in hours	Day Activity %	Night Length activity in hours	Night Activity %
Nov. 15th	1·4	16	6·9	45
16th	1·2	14	6·3	41
17th	1·4	16	7·6	49·5
18th	1·8	21	7·1	46
19th	1·2	14	6·4	41·5
20th	0·9	10·5	6·8	44
21st	1·3	15	7·4	48
22nd	1·2	14	7·3	46·5
23rd	1·3	15	7·7	50
24th	1·0	11·5	7·8	51
25th	1·4	16	6·9	45
26th	1·4	16	6·6	43
Average	1·3	15 (10·5–21)	7·0	45·8 (41–51)

Average % difference   **30·8**

Total average activity in 24 hours   8·3

% average activity in 24 hours   34·5

Exp. B

Date	Day Length activity in hours	Day Activity %	Night Length activity in hours	Night Activity %
Nov. 2nd	2·9	31	9·2	63
3rd	2·2	23·5	7·4	51
4th	2·9	31	7·7	53
5th	2·9	31	7·8	53
6th	2·4	25·5	7·1	49
7th	2·3	24·5	7·1	49
8th	2·1	22	7·0	48
9th	2·0	21	6·9	47
10th	2·4	25·5	6·3	43
11th	1·9	20	6·0	41
Average	2·2	25·5 (20–31)	7·25	49·7 (41–63)

Average % difference   **24·0**

Total average activity in 24 hours   9·45

% average activity in 24 hours   39·5

Exp. D

Date	Day Length activity in hours	Day Activity %	Night Length activity in hours	Night Activity %
Nov. 29th	1·6	21	8·1	51
30th	3·1	38	9·1	58
Dec. 1st	1·9	23	7·2	45·5
2nd	4·0	49	7·3	46
3rd	3·7	45	7·5	47·5
4th	2·2	27	8·8	60
5th		(No record)		
6th	4·3	52	6·6	42
7th	2·3	27	3·6	23
Average	2·9	35 (21–52)	7·4	46·6 (23–60)

Average % difference   **11·6**

Total average activity in 24 hours   10·3

% average activity in 24 hours   43·0

The average lengths of day and night in hours during the above experiments were:

Exp.	Day	Night
A	10·0	14·0
B	9·4	14·6
C	8·6	15·4
D	8·2	15·8

The 24-hour rhythm has its peak immediately after sunset. This is shown in Table II and Fig. 2 which give the average amount of activity per hour. It will be seen that, although the vole was fed at different times and with different food (Table I), the peak is well marked and occurs at the same time in each case. A better conception of the 24-hour rhythm is obtained if the influence of the short rhythm is eliminated by smoothing these figures $\left(\frac{a+b+c}{3}\right)$. The different feeding conditions were imposed on the voles for these experiments with a view to determining how the availability of fresh food and time of feeding affect the long rhythm. It is clearly shown in Fig. 2 that this has not altered the time of maximum activity. It seems therefore that the long rhythm is not easily altered except by the influence of light conditions. The average amount of activity falls away slightly during the night while after sunrise it is much reduced, falling below the average for the 24 hours. The percentage differences between day and night activity are shown in Table III. The influence of the different feeding conditions is well shown by these, notably between experiments A, B, C and D; in Exp. D the vole was fed twice a day on excess fresh food (Table I) and the amount of activity increased during the day, bringing the difference down to 11·6 per cent., whereas in the other experiments the differences were 30·5, 24·0 and 30·8 per cent. respectively.

During May, 1933, a series of records was taken of three voles; one in normal light and two in total darkness. The latter were kept in large boxes which effectively excluded light. After 24 days under these conditions the two voles had retained the 24-hour rhythm. Although the rhythm was some-what different in character, the peak occurred about the same time, i.e. just after sunset. The relative amount of activity for the "day" and "night" remains more or less the same, but in each case there is an average increase of about 1 hour over the 24 hours. The vole in normal light had a rhythm similar to that shown by the other two in the first part of the experiment. These experiments point to the existence of an internal rhythm that is adjusted throughout the year to the time of sunset and sunrise, and therefore fall into line with the work of Johnson on *Peromyscus*.

IV. Summary.

Experiments on the activity rhythms of *Microtus* show that it has a short 2- to 4-hour rhythm of feeding activity and a longer 24-hour rhythm with its peak following sunset and a higher average of activity at night. Voles kept in total darkness for 24 days maintained both rhythms.

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HABITAT SELECTION IN BIRDS

WITH SPECIAL REFERENCE TO THE EFFECTS OF AFFORESTATION ON THE BRECKLAND AVIFAUNA

By DAVID LACK, B.A.

(With Plates VIII, IX.)

CONTENTS.

INTRODUCTION.

THERE is an ever-growing mass of literature on the subject of bird distribution, but it is almost without exception purely descriptive. It seems to have been assumed that one of three essentials, suitable climatic conditions, sufficient food, or a safe nesting place, is limiting the bird directly, although almost no investigations have been made to determine which of these factors might be concerned in a particular case. Perhaps the most important contribution is that of Palmgren (1930), who tackles the problem from an ecological point of view based on most careful and detailed observations, but is in most cases unable to explain satisfactorily the bird distribution by means of these factors.

The recent afforestation of the Breckland heaths with pines affords an interesting experiment in this respect. In an attempt to explain the observed distributions, the inadequacy of the above three essential factors was at once apparent, and it was necessary to introduce a new factor of a psychological nature, the importance of which has not previously been realised. An exception occurs to some extent in the work of Brock (1914), whose interesting discussion on the ecological relations of bird distribution has not attracted the attention it deserves.

The investigation of the Breckland avifauna was due in the first place to the suggestion of Dr A. Watt, of the Cambridge University Forestry School, who has been greatly interested in the floristic and faunistic changes which the afforestation has been producing. I am indebted to him for much helpful advice, for obtaining permission for me to work in the area, and for supplying me with a map of the new plantations. I am also deeply indebted to Charles Elton, N. B. Kinnear, Dr H. L. Lack, Dr T. G. Longstaff, and Dr W. H. Thorpe for their many helpful suggestions during the preparation of the manuscript.

PART I. THE BRECKLAND AVIFAUNA.

(1) *Botanical description.*

The Breckland is an area of sandy heaths on the borders of Norfolk and Suffolk, the areas worked being close to Thetford and Brandon. The locality names used are those of the one-inch Ordnance Survey Map of Thetford for 1914, the old names of the heaths and warrens now afforested being retained. Farrow (1925) describes the plant communities of the Breckland, and stresses the importance of rabbit attack as a factor in their distribution. From the ornithological standpoint a brief classification suffices for the areas worked:

(1) *Grass heath.* Grasses (*Festuca ovina* and *Agrostis vulgaris*) the chief plants.
    (a) Closely grazed turf with much bare sand; rabbits extremely common, e.g. Little Heath near Larling.
    (b) The grass longer and flowering; rabbits much less common, e.g. much of Lakenheath Warren.

(2) *Grass with bracken.* The commonest heath type in the areas worked.
    (a) Both grass and bracken (*Pteridium aquilinum*) of poor growth, e.g. parts of Lakenheath Warren where bracken was sparse and only knee high.
    (b) Much richer growth, e.g. Brettenham Heath where bracken was often over waist high.
        Occasional deciduous bushes or trees, usually birch (*Betula*), had grown up in some of these areas.

(3) *Heather heath.* Much less common than grass heath in the areas worked, and pure heather (*Calluna vulgaris*) was rare, bracken and at times grass being mixed with it, e.g. Roudham and Bridgeham Heaths.

(4) *Afforested areas.* The areas, first cleared of rabbits, have been planted with pines, mainly the Scots Pine (*Pinus sylvestris*), in long rows some 4–8 ft. apart with occasional rides.

The ground vegetation was fairly thick grass and bracken, with heather at times. The plantations of the same year were of variable thickness, and some of those first selected for observation proved of exceptionally poor growth; the results from these have been kept distinct. Even the best grown plantations did not retain uniform thickness over large areas, but the chief thinner patches could be avoided. Save that the 1926[1] plantation at West Tofts had grown exceptionally well (it proved as thick as any 1925 plantations observed), the thickest plantation of each year appeared to have grown at a fairly equal rate, so far as this could be estimated by allowing for the intervening years' growth. In P. 27 (four years old at the time of observation) the pines were some 4 ft. high. In P. 25 (six years old) they were often 8 ft. in height and the lower lateral branches of neighbouring trees overlapped. In P. 22 (nine years old) the trees rose to over 12 ft. and the lateral branches of neighbouring trees interlocked so as to make many places almost impenetrable. The surrounding ground vegetation did not seem as yet to have been significantly affected by the trees. The examples of the different plantations worked are given in Appendix I. P. 22 is the oldest in Thetford Chase.

(2) *Method of observation and recording.*

The main observations were made between June 19th and 27th, 1931[2]. This was unavoidably a little late in the year, but most pairs of birds still held breeding territories, and any young which had left the nest were usually distinguishable from adults. The observer walked steadily through the areas selected, recording every breeding pair of birds seen on either side within some 20 yards. At least two counts were taken in each type of country, the subsequent counts being over fresh ground as distant as possible from the first to minimise the influence of local irregularities of distribution. No counts were taken on the edges of areas, since here the population might be affected by the type of vegetation adjoining. This method admittedly gives only approximate figures, but these are sufficiently accurate for the purpose.

The actual counts are given in Appendix I. For comparing the populations of different areas the number of pairs of each species is expressed as a percentage of the total bird population. No percentages are based on a total population under thirty-five pairs save for the P. 27 at Bromehill (eighteen pairs), while most refer to over fifty pairs. This percentage method was designed to give comparative figures. The total bird population densities could only have been estimated with extreme difficulty, and then only approximately.

For simplicity, birds are referred to by their popular names, the Latin names of all species in the text being given in Appendix III.

(3) *Distribution of the birds.*

Tables I, II, III summarise the effects of the afforestation on the bird life. Table I shows how the species met on typical heath land have been steadily replaced by a new avifauna, members of which first appeared in the

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[1] The year refers to the year of planting. In future the abbreviations, P. 28 to P. 22, are used for plantations of the years 1928 to 1922 respectively.

[2] The main plantations were counted again from June 9th to 12th, 1933. Unless otherwise stated observations refer to 1931.

Table I.

| | Percentage of bird population formed by | |
| | A. Species found on the heaths | B. Species found only in the afforested areas |
Type of vegetation		
1. Heaths	100	0
2. P. 27 and later, 4 years old and younger	100	0
3. P. 26, 5 years old		
(a) Poor growth	95	5
(b) Rich growth	60	40
4. P. 25, 6 years old		
Fair growth	60	40
5. P. 24, 7 years old		
(a) Fair growth	35	65
(b) Good growth	15	85
6. P. 23, 8 years old		
Good growth	5	95
7. P. 22, 9 years old		
Very fair growth	×	100

"A" includes Wheatear, Stock Dove, Stone Curlew, Lapwing, Skylark, Meadow Pipit, Stonechat and Whinchat. "B" includes Willow Warbler, Whitethroat, Wren, Dunnock, Blackbird, Goldcrest, Chaffinch. (Whitethroat, Wren and Willow Warbler were only exceptional on the heaths.)

Note. The figures are calculated, as in Tables II and III, to the nearest 5 %. × indicates a figure lower than 3 %.

Table II.

Percentage of bird population formed by

Type of vegetation	Wheatear	Stock Dove	Stone Curlew	Lapwing	Skylark	Meadow Pipit	Whinchat	Stonechat
Grass turf	40	5	15	5	30	.	.	.
Thin grass	5	×	5	5	65	20	.	.
Thin grass and thin bracken	.	.	×	×	65	25	×	×
P. 27, 4 years old Poor growth	.	.	.	.	50	30	20	.
Grass and thick bracken	.	.	.	.	55	10	25	5
P. 27, 4 years old Good growth	.	.	.	.	35	30	20	20
P. 26, 5 years old Poor growth	×	.	×	.	40	40	10	×
P. 25, 6 years old Fair growth	.	.	×	.	25	15	10	5
P. 26, 5 years old Good growth	.	.	.	.	15	20	25	.
P. 24, 7 years old Fair growth	.	.	.	.	15	10	5	×
P. 24, 7 years old Good growth	.	.	.	.	10	×	5	.
P. 23, 8 years old Good growth	.	.	.	.	.	5	.	5
P. 22, 9 years old Fair Growth	.	.	.	.	.	×	.	

Table II (cont.).

Percentage of bird population formed by

Type of vegetation	Willow Warbler	White-throat	Wren	Dun-nock	Black-bird	Chaf-finch	Gold-crest	Song Thrush
Grass turf	·	·	·	·	·	·	·	·
Thin grass	·	·	·	·	·	·	·	·
Thin grass and thin bracken	·	·	·	·	·	·	·	·
P. 27, 4 years old Poor growth	·	·	·	·	·	·	·	·
Grass and thick bracken	·	×	×	·	·	·	·	·
P. 27, 4 years old Good growth	·	·	·	·	·	·	·	·
P. 26, 5 years old Poor growth	5	·	·	·	·	·	·	·
P. 25, 6 years old Fair growth	30	5	5	·	·	·	·	·
P. 26, 5 years old Good growth	30	5	5	·	·	·	·	·
P. 24, 7 years old Fair growth	40	10	10	5	·	·	·	·
P. 24, 7 years old Good growth	50	15	5	10	5	·	·	·
P. 23, 8 years old Good growth	50	20	10	5	·	5	×	·
P. 22, 9 years old Fair growth	65	5	5	10	10	·	5	·

Note. All the common breeding species have been included (see Appendix I for full data) but the following were omitted as their occurrences were too few and irregular: Common and Red-legged Partridges (both decreasing as the trees grew up), Pheasant (increasing as the trees grew up), Linnet, Lesser Redpoll, and Mistle Thrush (possibly breeding in older plantations, but not proved), and Yellow and Reed Buntings, Wood Lark, Tree Pipit, Yellow Wagtail, Sedge Warbler, Grasshopper Warbler, Robin, Cuckoo and Nightjar. Also the Ringed Plover, found locally on sandy heaths, was not met in the areas worked. Counts in plantations younger than P. 27 are omitted. The birds here were those of the ground vegetation.

five-year-old plantations, assumed a majority two years later and were present to the almost complete exclusion of the original avifauna two years after this. Thus in about five years the avifauna has changed almost completely in character. Table II is the same in an expanded form.

In Table II the types of vegetation have been arranged in an order of increasing height (which is at times at variance with the age of the plantations). There were marked changes in bird distribution in the series of four heath types given, Wheatear, Stock Dove, Stone Curlew and Lapwing dying out, while Stonechat and Whinchat, which were absent from the barest heaths, increased. In the thickest bracken a few Whitethroat and Wren were found.

The plantations continue this series. The two most marked features were the steady decrease of Skylark and Meadow Pipit (which had already begun in thick bracken) and the appearance and rapid increase of the Willow Warbler. Stonechat and Whinchat at first increased, reached their maximum in the

four- and five-year-old plantations, and then decreased. The Whitethroat and Wren appeared in the five-year-old plantations and became a little commoner in older plantations. Finally Blackbird and Dunnock first appeared in the seven-year-old plantations, the Goldcrest and Chaffinch in the eight-year-old plantations, but had not by then attained importance.

Table III.

Type of vegetation	Percentage of bird population formed by					
	Sky-lark	Meadow Pipit	Whin-chat	Stone-chat	Willow Warbler	White-throat
P. 27, 6 years old Poor growth	30	45	5	.	15	.
P. 27, 6 years old Good growth	10	5	10	.	55	.
P. 26, 7 years old Poor growth	25	10	5	.	45	10
P. 25, 8 years old Fair growth	10	×	10	.	40	10
P. 26, 7 years old Good growth	.	.	10	.	60	5
P. 24, 9 years old Fair growth	.	.	.	.	60	15
P. 24, 9 years old Good growth	.	.	.	×	40	5
P. 23, 10 years old Good growth	.	.	.	.	35	5
P. 22, 11 years old Very fair growth	.	.	.	.	40	•

Type of vegetation	Percentage of bird population formed by					
	Wren	Dun-nock	Black-bird	Chaf-finch	Gold-crest	Song Thrush
P. 27, 6 years old Poor growth	.	.	.	.	.	.
P. 27, 6 years old Good growth	5	5	10	.	.	.
P. 26, 7 years old Poor growth	5	.	.	.	.	.
P. 25, 8 years old Fair growth	5	10	10	×	.	×
P. 26, 7 years old Good growth	10	5	10	5	.	5
P. 24, 9 years old Fair growth	10	.	10	5	5	.
P. 24, 9 years old Good growth	15	10	10	20	×	5
P. 23, 10 years old Good growth	15	5	10	15	×	10
P. 22, 11 years old Very fair growth	15	15	10	15	5	5

Table III shows the populations in 1933 of the same plantations counted in 1931. The main interest is in P. 23 (now ten years old) and P. 22 (eleven years old). The original heath fauna has here quite disappeared, and the Whitethroat

Photo. David Lack

Phot. 1. The bare rabbit-grazed Little Heath.

Photo. David Lack
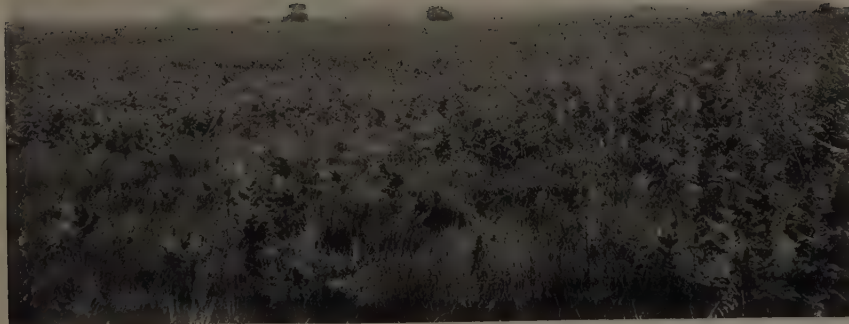
Phot. 2. Brettenham Heath. Grass and fairly thick bracken.

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(never very common) has nearly gone. The Willow Warbler was evidently at its maximum in the eight- and nine-year-old plantations, and has now begun to decrease, while the more recent arrivals, Blackbird, Goldcrest, Chaffinch and Song Thrush, are tending to increase.

The other plantations bear out the main conclusions of 1931, and show that the changes previously described occur in each individual plantation as the trees grow higher. The discrepancies observed when plantations of the same age are compared for the two years are due mainly to differences in the rate of growth of the trees, which was at times very marked. This especially applied to the continued exceptional growth of the P. 26 at West Tofts, where Blackbird, Song Thrush and Chaffinch were recorded in 1933, although no six-year-old plantation in 1931 had these species.

It must be noted that the distribution of the birds was always irregular. Only when large areas are considered are the changes really apparent. Fortunately, as can be seen from the tables, the changes in distribution occurred extremely rapidly, a new fauna having colonised and an older one died out within five years. Also, in 1933, where much of an eight-year-old plantation had been burnt down three years before, the original heath fauna of Skylark, Meadow Pipit, Stonechat and Whinchat was found to be present in normal strength, having recolonised within this time.

However, there was a slight lag in both the disappearance and the colonisation of species. For example, the Stone Curlew persisted to breed in plantations five and six years old, haunts with higher vegetation than that normal to the species. Also the most recent forms to colonise the plantations were sometimes irregular in their appearance, having not yet appeared in certain plantations apparently as suited to them as those in which they did occur. Thus, in 1931, P. 22 and P. 23 afforded very similar conditions, but the Blackbird was present only in P. 22, the Chaffinch only in P. 23. By 1933 both had appeared in each.

The few more mature Breckland pinewoods gave little idea of the future avifauna of the afforested areas, since they were too few and small, often rather open, and usually contained some deciduous trees. The Chaffinch was much the commonest species, and the Goldcrest, Coal and Marsh Tits also occurred, with others. The Willow Warbler was scarce, and found only round the more open spaces. Three or even two centuries ago the Breckland was a sandy and treeless waste, so that a number of the heath birds must have colonised fairly recently, while some members of the older fauna, including the Great Bustard, have vanished. Further, owing to extensive game preservation in the neighbourhood, birds of prey are now almost extinct, and hence the small Passerine birds are perhaps more abundant than they would otherwise be. The avifauna of the heaths at present seems relatively static, but in the areas with more mature trees colonisation by such species as Wood Lark and Crossbill seems to be still taking place.

The above is only a summary of bird distribution on the Breckland and the changes due to afforestation. Where of special interest, further details will be found in the following discussion.

<div align="center">PART II. FACTORS LIMITING DISTRIBUTION.</div>

The rapidity of the changes in the avifauna resulting from the afforestation of the heaths indicates that the immigrants, especially the Willow Warbler, were abundant in the surrounding country and were kept back from spreading only by lack of suitable habitats. The two most obvious factors concerned in the changes in distribution are food and nesting requirements. A third, that of enemies, can be ruled out, since man has destroyed almost all the bird and egg-eating animals of the district.

<div align="center">(1) <i>Species limited by nesting requirements.</i></div>

The Wheatear was common on the open heaths, where it was found nesting exclusively down rabbit burrows. It did not occur in the afforested areas, which, being rabbit proof, were devoid of burrows. But the bird was once found breeding in a four-year-old, and once in a five-year-old plantation, both of which seemed typical save that an old burrow had persisted. These cases show that the young plantations were otherwise suitable and that nesting requirements alone limited the bird's distribution. The same presumably applies to the Stock Dove, which also nested in rabbit burrows on the open heaths, but was not found in the young plantations. A pair of Coal Tits was found feeding recently fledged young in a seven-year-old plantation, and a pair of Marsh Tits was similarly employed in an eight-year-old plantation. This showed that, as one would expect from the birds' known habits, such areas were suitable with regard to food. But neither species nested in any young plantation. Since they appeared as soon as nesting was finished, this was clearly due to absence of the usual nesting sites, holes in trees or banks, of which there were none in the young plantations. This explanation could be tested experimentally by putting up artificial nesting boxes and seeing if the birds then colonised the plantations. This has not been done here. But nesting boxes have been put up in the young pine plantations of the Stadtwald of Frankfurt-on-Maine and here, in 1929, the writer found the Coal Tit breeding. It nested only in the boxes, thus confirming the conclusion that young pine plantations are suited to this species save for the normal lack of nesting sites.

The Meadow Pipit, common on every other heath, was absent from the bare rabbit-grazed Little Heath where its usual associate, the Skylark, remained common. Nesting requirements perhaps explain this, the former selecting rather thick ground vegetation, the latter much more open ground. In no further case were nesting requirements thought to be limiting distribution.

Where nesting requirements limit distribution it is commonly supposed that the limit is an absolute one, that no safe nesting place is available. Actually in the above cases (and probably in most others) the limit is due to the stereotyped nature of the bird's behaviour. There is nothing else to prevent the Wheatear from nesting in thick vegetation, which is the normal habit of the closely related Stonechat and Whinchat, or the Coal Tit from building a nest on a fir branch, or the Meadow Pipit from nesting in such bare places as the Skylark. It is because their *accustomed*, not because all, nesting sites are absent that they disappear or fail to colonise. This lack of adaptability is in keeping with the fundamentally instinctive nature of bird behaviour.

On the shingle area of Dungeness, Kent, where the Wheatear's usual nesting sites are absent, the bird does occur, nesting under derelict metal objects, and occasionally among the roots of a gorse bush, or in a depression in the open (Ticehurst, 1909). In this area, which has existed a great many years, the bird's habit has become modified, rendering colonisation possible. Hence on occasion the usual nesting site may be modified, but such cases are rare. This occurrence is of special interest since the bird has not, as yet, modified its habits in this direction on the Breckland, though it would be advantageous for it to do so.

(2) *Tree Pipit.*

The Tree Pipit occurred regularly in open heath country identical with that frequented by the closely allied Meadow Pipit provided one or more fairly tall trees were present. Owing to this last condition it was absent from many localities where the Meadow Pipit was abundant. What factor could cause this? Nesting requirements are ruled out, being identical with those of the Meadow Pipit. Both nest on the ground. Nor was the Tree Pipit observed feeding in trees, and analyses of the food from various parts of England (Jourdain, 1920) show the requirements of both species to be the same. Protection from enemies is ruled out since both species nest and roost on the ground, and in any case appear to have no enemies on the Breckland. One cannot postulate physiological or other adaptations of the species to their slightly different environments, since the difference at times rests solely in the presence of a single tree, occupying but a small part of the breeding area. Further, in a treeless part of Cambridgeshire, the writer found a pair of Tree Pipits breeding close to a telegraph pole. The only use to which the tree, and in the last case the pole, is put by the Tree Pipit is as a perch to which to fly down towards the end of its aerial song. The Meadow Pipit has a very similar song but normally ends it on the ground.

To ornithologists imbued with teleological views of bird distribution, it may seem surprising that the Tree Pipit should be prevented from colonising the Breckland heaths solely through a psychological requirement, correlated with the singing habit, for a tall tree. But this is in keeping with the instinctive

nature of bird behaviour commented on in the last section. Singing is an important part of bird behaviour. That a bird should be unable to modify its habits in this direction is little more remarkable than its failure to do so with regard to its nesting site demonstrated previously.

(3) *Willow Warbler.*

The Willow Warbler, normally absent from the Breckland heaths, colonised the young plantations when these were five years old, increased rapidly, and was the commonest bird in the seven- to nine-year-old plantations. What requirement, absent from the heaths, was supplied by the young plantations? On the traditional view of bird distribution one might suppose this factor to have been thick cover (for moving in which the bird seems well adapted), nesting sites, and/or suitable food, all of which might be different in the young plantations from what they were on the heaths. Actually it proved to be none of these. Though absent from most heaths, the Willow Warbler occurred on a number of the most thickly vegetated ones where a bush (usually a birch or thorn) 5 ft. or more in height, and often isolated, had sown itself. The surrounding heath was quite typical and here the bird nested (i.e. away from the bush) and obtained the great bulk, if not all, of its food. The bush was used mainly for singing from, but the male spent much of his time there, perhaps even feeding, though the supply from the bush could not have been significant.

The latter cases show that the Willow Warbler could exist on the thickly vegetated heaths so far as food and nesting requirements were concerned. Only the scarcity of a taller bush had prevented it from spreading over such areas. It was clearly only this last essential that the young plantations supplied. Hence, as in the previous cases, distribution was limited by a psychological requirement. This was correlated with the singing habit, though perhaps not exclusively, since the Willow Warbler frequented its tree at other times also. It may be noted that the young plantations introduce a new insect fauna. An analysis of the food of the Willow Warblers breeding in the plantations would probably have shown the presence of insects not found on the heaths. The above discussion shows the fallacy of concluding from this that the heaths could not supply the Willow Warbler with suitable food.

(4) *Reed and Yellow Buntings.*

The Reed and Yellow Buntings are two species of the same genus both common on the Breckland, the former in marshy districts, the latter in drier districts, along the hedgerows and the edges of heaths, etc. The two showed almost no overlap of habitat. What factor or factors caused this marked difference? The nesting sites of the two species seemed similar, both being in thick vegetation on or slightly above the ground. Their breeding habits seemed similar. So far as known neither possessed structural or other adaptations to
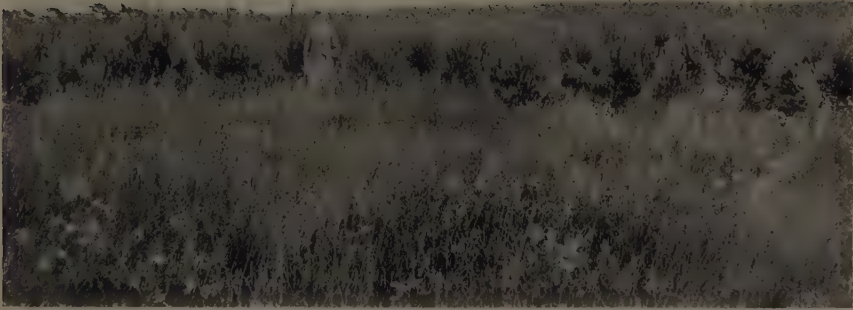
Photo. David Lack

Phot. 3. Fairly well-grown P. 25. Six years old. (*Pinus sylvestris.*)

Photo. David Lack

Phot. 4. Well-grown P. 23. Eight years old. (*Pinus sylvestris.*)

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its particular habitat. The food of the two species is mainly vegetable, especially seeds, while in summer insects of many orders are taken. The sole difference is that the Reed Bunting mainly eats *marsh* plants and insects, the Yellow Bunting mainly those of drier situations (Jourdain, 1920). Since both have such a varied diet one cannot suppose that so slight a difference, even if appreciable to the birds (which is doubtful), could cause such a marked difference in distribution. It seems clear that both species utilise the food that happens to be commonest in their respective habitats.

The situation was made more remarkable by the discovery of one pair of Reed Buntings which successfully reared a family on Brettenham Heath in a typical Yellow Bunting habitat several miles from any marsh. This renders it extremely improbable that there existed even slight adaptive, including physiological, differences between the two species (whose presence would be hard to ascertain); and that such factors, acting through an intensive competition, have produced the present distribution.

There therefore seems nothing in the environment to compel the difference in distribution. The remaining possibility is a psychological factor. In the species previously considered a psychological limit could be correlated with a definite part of the bird's behaviour. In the present case there were no differences in the behaviour of the two species which could be correlated with differences in the habitats. The only remaining possibility is to suppose that the Reed Bunting, returning to its breeding ground in spring, instinctively selects its ancestral habitat, a marsh, the Yellow Bunting selecting drier ground for the same reason.

The last is really not at all an improbable hypothesis, though it does not seem to have been advanced in connection with bird distribution before, save that Brock (1914, p. 41) clearly had a psychological factor in mind in his "environmental bias." Hereditary instinct controls the design of the bird's nest, the materials used, and the site adopted, each species adhering to its own particular type, though the differences between closely related species cannot be explained teleologically. When instinct controls such matters, it would indeed be surprising if it did not control the type of ground selected by the bird for a breeding territory. To this instinctive selection by the bird of the type of habitat frequented by its ancestors, the term *habitat selection* will be given. It must be noted that the process of selection is considered instinctive. "Selection" has unfortunate anthropomorphic associations but no better term seems available. "Habitat preference" is open to the same objection, and further has been used by many writers (not only with regard to birds) in a much more general sense.

In winter the Reed and Yellow Buntings are usually in flocks scattered about the countryside. In early spring they return to the breeding grounds and the males take up prominent positions and sing (Howard, 1929). Although the birds are very mobile they do not at this season appear in every sort of

habitat, to give it a trial. Each species returns to its typical habitat, to account for which one must postulate the existence of habitat selection, that the birds can (instinctively) recognise their typical habitat. If the difference in distribution between Reed and Yellow Bunting is due to the existence of specific habitat selection, the exceptional occurrence of a pair of the former in the habitat of the latter must be considered due to an aberration from the normal behaviour. Such are well known to occur occasionally with regard to other instincts, such as nest-building. The occurrence does not invalidate the hypothesis of habitat selection. On the other hand, had the restriction of the Reed Bunting to marshes been due to the direct influence of an environmental factor, such an incident would be extremely difficult to explain.

(5) *Other species of the young plantations.*

The changes in bird distribution due to the growth of the young pines on the heaths have been described. Lack of space prevents a detailed analysis for each species, and some, for which the data obtained were insufficient to warrant any conclusions, will be omitted. *Nesting requirements*, apart from the few cases mentioned earlier, do not seem to have been the cause of any of the changes. Nesting sites typical of those normally selected by Stone Curlew, Lapwing, Skylark, Meadow Pipit, Stonechat, Whinchat, Common and Red-legged Partridge were still afforded by the young plantations after these species had disappeared. Nesting sites typical of those normally selected by Willow Warbler, Dunnock, Blackbird, Song Thrush, Goldcrest, Chaffinch, Robin and Pheasant (and probably Whitethroat and Wren) were available before (i.e. at a younger stage than) these species colonised.

With regard to *food*, while it is obvious that a bird must have a sufficient quantity of readily available food, the importance of its quality seems to have been greatly exaggerated by ornithologists. It has frequently been assumed that a species is limited to a particular habitat because its normal food seems similarly restricted. Brock (1914) pointed out the fallacy in this, but his statement has been ignored. Thus Coward (1928), discussing the distribution of the Sedge Warbler, says "the presence of water in lake, small pond, river, ditch or marsh, is all it requires for it feeds upon gnats, midges and other dipterous flies whose early life is aquatic." Numerous similar statements could be cited.

In most such cases at least the analyses have been insufficient to show that the distribution of the food was restricted to the habitat of the bird. Were this proved, it would then be necessary to show that the bird refuses to take the types of food available to it beyond the borders of its habitat, which seems never to have been attempted. Further, there is now considerable evidence that most birds have an extremely varied diet; see, for example, Jourdain (1920), McAtee (1932). Food preferences undoubtedly exist in birds, as shown for instance by Mottram (1918), but present evidence is in favour of

supposing that they are readily broken through and hence are unimportant in limiting distribution. Exceptions to this probably occur in birds adapted for obtaining very special types of food, but such seem to be rare.

With regard to the Breckland birds, stomach analyses would of course show that the Skylark and Meadow Pipit were eating mainly the insects of the heaths; Willow Warbler, Blackbird, Goldcrest and others mainly those of the plantations. This proves nothing more than that each species feeds on the commonest available insects in its habitat. Analyses of the food of the species concerned (Jourdain, 1920) show it to be extremely varied, insects of almost every sort, some other invertebrates, and a variety of vegetable matter being taken by each. It therefore seems unlikely that the insects of the young plantations would be less acceptable than those of the heaths to the birds of the latter, or that the birds of the plantations, especially with the proved case of the Willow Warbler before one, would find the insects of the heath unsuitable. The following cases further suggest, if they do not prove, that food was not concerned.

The Common and Red-legged Partridge decreased, the Pheasant increased, as the plantations grew up. Their food is said to be similar. The Chiffchaff was never recorded from the young plantations, though its food does not differ significantly from that of the closely allied Willow Warbler. The Whinchat and Stonechat were common on the most thickly vegetated heaths; they were somewhat more common in the four- and five-year-old plantations, but decreased in those older than this. Any new food introduced by the young pines could not have been the cause of both the increase and the decrease. Again, it seems unlikely that there should have been insufficient food for the Goldcrest in the seven-year-old and younger plantations, when there was sufficient in the eight-year-old which were merely a little taller. Stone Curlew, also Meadow Pipit, tended to linger on in the young plantations though the habitat was no longer that normal to the species (presumably due to the habit demonstrated in many birds of returning each year to breed in the same place). That such birds could rear their young successfully indicates that the food supply was still sufficient, and hence was presumably not concerned in the disappearance of their fellows. Lastly, the Song Thrush was sometimes observed feeding on the heaths, showing that the latter could supply at least a part of its diet.

In conclusion, although food is clearly important in controlling the density of the whole bird population in any area, in not a single case on the Breckland was there evidence for supposing that it limited the distribution of any particular species.

      *   *   *   *   *   *   *

From the changes in distribution which occurred it is apparent that the birds were affected far more by the height of the vegetation than by its nature. This is shown specially well in the Stonechat and Whinchat, which were

equally common in vegetation of similar height whether this was bracken or young pines. This suggests strongly that once again one is dealing with a *psychological factor*. The particular height (within limits) of the vegetation does not seem to affect any of the birds' essential requirements, but in some cases it is correlated with particular habits. Thus the Stonechat and Whinchat use the tops of the vegetation as perches from which to sing and to make aerial flights after food. Their nests, however, are on, or close to, the ground. The Blackbird sings and nests well off the ground, so in these habits the height of the vegetation may be significant, but it feeds on the ground. In various other species nesting, singing, feeding, and other activities can be correlated with the height of the vegetation. In no case does the correlation seem more than a psychological one. Thus, so far as one can see, no disadvantage would be incurred if the Stonechat sang on the ground and the Blackbird nested there (which is the normal habit in certain close relatives of each species).

In many cases, however, the dependence of distribution on the height of the vegetation cannot be correlated with any particular habit, this especially applying to species disappearing as the vegetation grows higher. The Skylark, for instance, sings in the air and nests and feeds on the ground. These are, in essentials, unchanged in young plantations from which the bird has vanished. The same applies to the Stonechat which nests on the ground, feeds in the air from a perch (and also on the ground), and sings from a perch. These are still supplied in young plantations from which the bird has gone. Many similar cases could be cited.

Through the complete inadequacy of other factors one has to postulate, as in the case of Reed and Yellow Buntings, the existence of specific *habitat selection*. The arguments brought forward for its existence in these species, based on the immediate adoption of the typical habitat in spring, apply to these other species also. Now, selection of the ancestral habitat implies recognition, and one would therefore expect habitat selection to be correlated with the conspicuous features of the habitat. The height of the vegetation is certainly one of the most conspicuous features of the habitat on the Breckland, and the close dependence of distribution on it, irrespective of whether it was correlated with any essential avian requirements, is just what one would expect if distribution was being limited through habitat selection.

The nature of a bird's normal habitat, i.e. that determined by habitat selection, can be estimated only by studying its distribution over a wide area. The distributions on the Breckland certainly conform with the known distributions of the species elsewhere in Britain. Thus the complete absence of the Chiffchaff from the young plantations can scarcely be explained save on habitat selection, for the bird is almost identical in size, plumage, habits, and food requirements with the Willow Warbler, which is the commonest bird in the plantations. The Chiffchaff frequents somewhat taller vegetation than the Willow Warbler throughout Britain. Again, the Pheasant increases,

the Common and Red-legged Partridges decrease, as the plantations grow up, which can scarcely be explained save on habitat selection, since their food, nesting habits, adaptation to running, etc., are so similar. Throughout Britain, the former frequents woods, the two latter open ground. Again, the Meadow Pipit and Stone Curlew frequent open country throughout Britain: their disappearance from the young plantations must surely be due to habitat selection, not to a direct effect of the environment, since those which lingered on (through another instinct, that of returning to breed in the same place each year) were able to thrive.

(6) Ringed Plover.

The case of the Ringed Plover is exceptional. The bird was breeding on a few of the barest sandy heaths, but was not found where the vegetation grew at all thickly. Its absence from the latter areas could not well be correlated with its essential nesting requirements or its adaptation to running, and it seems unlikely that food supply could have been concerned. Habitat selection could account for it, however, since the bird is normally restricted to bare sand and shingle (out on the foreshore). Since the Ringed Plover normally frequents the foreshore, its presence inland on the Breckland requires explanation. Certain coastal plants, insects, and mollusca are also found on the Breckland which, with the sandy nature of the terrain, show that the area was originally one of coastal sand dunes which later became cut off from the sea. The changes evidently proceeded sufficiently slowly for the Ringed Plover not to be driven away. This may be compared with the Stone Curlew and Meadow Pipit, which lingered on in the young plantations for a short while, but here the changes in habitat were evidently far too rapid to produce any permanent modification. The habitat preference of the Ringed Plover has been modified only locally. It does not normally frequent the sandy inland heaths of Britain, although to-day these seem to offer the same conditions as those in which it occurs on the Breckland. Lönnberg (1932) describes a number of wading birds which, normally coastal, are similarly " relict " inland in Central Asia. Here also, only the past history of the area explains their occurrence.

(7) Summary of Part II.

Various species limited by nesting requirements show the importance of the psychological factor in bird distribution. This is further emphasised by the absence of certain species from areas otherwise suitable which did not supply them with a singing perch. In many other species a consideration of the birds' essential requirements failed to account for the limits of distribution, nor could a psychological factor correlated with a definite habit provide explanation. It was necessary to introduce the idea that each species instinctively

selects its ancestral habitat, the evidence for the existence of habitat selection being based on the following points:

(1) Other factors were completely inadequate to account for more than a few cases of distribution on the Breckland.

(2) There is strong likelihood that in so highly organised an animal as a bird such a mechanism would exist.

(3) In spring when birds take up their breeding quarters, they normally appear straight away in the typical habitat. Had there been no habitat selection, one would have expected them to attempt to breed in other habitats.

(4) Distribution on the Breckland frequently depended on the conspicuous features of the habitat, irrespective of whether these were correlated with the birds' essential requirements. Habitat selection implies recognition of the typical habitat, which one would expect to depend on its conspicuous features.

(5) Rarely a bird broke away from its ancestral habitat and bred with apparent success elsewhere. This affords the best evidence that a bird's restriction to its habitat is psychological. Just as the nesting of the Wheatear on Dungeness in the open shows its normal selection of a hole to be due to habit, so the presence of the Ringed Plover on the Breckland heaths shows its normal restriction to the foreshore to be due not to environmental necessity but to a psychological factor, i.e. instinctive habitat selection.

PART III. GENERAL DISCUSSION OF HABITAT SELECTION.

(1) *Features on which it depends.*

The height of the vegetation is of course by no means the only feature of the environment correlated with habitat selection, which may clearly depend on a number of features. In the Reed and Yellow Buntings the field data did not permit analysis. In other species discussed in Part II the influence of the height of the vegetation could be isolated from other features, hence its prominence in the discussion. It is obvious also that two species may occur in the same locality because of very different features; for instance, both the ground-frequenting Meadow Pipit and the Goldcrest occurred in an eight-year-old pine plantation.

(2) *Relation to particular habits.*

The distribution of the Tree Pipit was limited by the presence of a tall tree. This could be correlated with the singing habit, but the bird sometimes descends to the ground instead of to a tree when singing, and it seems better to consider the limitation as due rather to habitat selection, perhaps strengthened by the close association of the tree with a particular habit. This is brought out by the birds, mentioned later in Part II, in which the height of the vegetation could be correlated with more than one habit, while in most it was correlated with no particular habit, though still the important factor in dis-

tribution. Instincts govern the bird's selection of all its requirements, nesting site, nesting material, food, etc. These instincts will be satisfied in the normal habitat. It is only under unusual conditions, such as a heath with no rabbit burrows, or a pine wood with no holes in the trees, that these instincts, rather than habitat selection, limit distribution. The situation is of course different in the many birds (unrepresented in the areas worked) whose feeding and nesting habitats are quite distinct, such as the cliff-nesting sea-birds. Probably in these forms one can no longer speak of a general habitat selection, since the activities correlated with nesting, and those correlated with feeding, refer to separate areas. Such cases are to be discussed in a future paper.

(3) *Biological advantage.*

Instances have been given where the existence of habitat selection prevented a bird from colonising, or caused its disappearance from, an area where it could have bred successfully. But although it restricts distribution, habitat selection insures a suitable habitat (the ancestral one). A bird has no means of knowing whether any other habitat would or would not be suitable to it. Habitat selection replaces the chance dispersal found in many primitive animals, in which the individual may happen on a suitable habitat but often does not.

(4) *Breaking away from the ancestral habitat*[1].

The freak occurrence of the Reed Bunting on a heath, the lingering of Meadow Pipit and Stone Curlew in the young plantations, and the presence of the Ringed Plover inland on the Breckland show that a bird may break away from its habitat-selection instinct. But such cases are rare. The Green Woodpecker shows particularly well the difficulty birds have in breaking away from the ancestral habitat. This species, though specialised like all Woodpeckers for climbing and feeding on tree trunks, has so far broken away from the ancestral habit as to feed on the ground, especially round ant hills. However, it still returns to a tree trunk to nest. Hence it has not, as yet, spread into the treeless areas which its altered feeding habits would have made suitable. The species which have colonised human dwellings and agricultural land are of special interest with regard to breaking away from the ancestral habitat. This subject is too large to be discussed here, but it may be noted that in some cases at least there need have been very little modification. From the bird's standpoint, if not our own, the new habitat may be similar to the ancestral.

[1] Observations made with B. B. Roberts in Iceland in 1933, to be published later, somewhat modify this section. It was found where more birds were available than their typical habitat could provide for, that they became less restricted in the type of breeding ground which they selected. Hence one should probably speak rather of the modification of a habitat preference than of the breaking away from the type of the ancestral habitat.

(5) *Influence on density of population.*

The influence of habitat selection on the density of the bird population is another subject which can be but briefly mentioned. Its importance was well shown in the five-year-old plantation at West Tofts. This seemed a fairly uniform habitat, but in the more open parts the Meadow Pipit and Skylark were the commonest birds, the Willow Warbler being scarce, whereas in the taller and thicker parts this distribution was reversed. Intermediately, Stonechat and Whinchat were the commonest types. Thus, as a result of their differing habitat preferences, the distribution of the birds varied very appreciably in a habitat which, the trees being all of the same age, exhibited a greater uniformity than that of many natural environments. It is this factor which, as pointed out by Elton (1932) and Longstaff (1932), renders density estimations from a bird census of such doubtful scientific value.

(6) *Habitat selection and evolution*[1].

The distribution of Breckland birds seems explicable only on the assumption that each species selects its ancestral habitat, recognising it by conspicuous features. It remains to consider why different species should select different habitats; in particular why closely allied species should so often select similar but distinct habitats, which adjoin but scarcely overlap. The Meadow, Tree and Rock Pipits are cases in point; the Yellow and Reed Buntings another. Indeed it seems a widespread phenomenon among Passerine birds in Northern Europe, although in England it often tends to be obscured by the influence of man, who has modified a habitat so that it satisfies the requirements of more than one species. Thus the Mistle and Song Thrushes both frequent gardens in England, but in their unmodified haunts in Central Europe the writer found them in separate habitats.

While admitting that habitat selection controls the distribution to-day, through ability to recognise the ancestral habitat, one might consider that the original reason for the differences in distribution were correlated with adaptations, adaptations which still exist but which do not meet the eye. Against this is that in not a single case, so far as the writer knows, has differential adaptation to the respective habitats been proved between closely allied species of Passerines. It is a very big assumption that in every case these adaptations exist but are too small to be appreciated, and in such cases as that of the Tree and Meadow Pipit the idea of differential adaptation, at least as applied to the Breckland distribution, seems untenable.

If there is no differential adaptation to the different habitats an explanation

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[1] This section, like most of the paper, refers to Passerine birds, the order to which most of the Breckland species belong. Some European Seabirds, Ducks and Waders are to be discussed in a later paper on Icelandic birds. In the Ducks at least, the situation seems very different from that here set forth for the Passerines.

is still possible. Consider a species whose range included two types of habitat which, while presenting the same essential requirements, differed markedly in their appearance; for instance, a Pipit frequenting bare meadow land and also similar meadow land with large trees. The conspicuous features (those correlated with habitat selection) are different and, since distribution depends on habitat selection, one could conceive that the individuals breeding in each type of habitat would tend to select the same one when they returned in spring. In this way two groups might become isolated, and eventually split into two species (i.e. Meadow and Tree Pipits). In the North Temperate regions the habitats of closely allied species of Passerines often afford the same essential requirements but differ markedly in their appearance. The view that such species have become segregated from each other through differential habitat selection is admittedly hypothetical, but would explain this and also the absence of differential adaptations to the respective habitats. The importance of isolation in the production of species is widely recognised, and the existence of habitat selection suggests how isolation could be effected between forms whose geographical range coincided.

Not only do different species of the same genus seem to live in the different types of the same sort of habitat, but the same is observed when higher groups are compared. Thus the Pipits and Warblers occupy distinct but adjoining habitats, suggesting that they and other families of Passerine birds also became separated by a division of the habitat which belonged to their common ancestor. Among higher groups the division is often less sharp. There has been longer time for modification to occur (for habitat preferences, though strong, are occasionally modified, as illustrated earlier) with the result that ranges overlap. Less closely related groups are somewhat differentially adapted to their habitats. The Pipit, for example, seems more adapted to progression in the open, the Warbler in thick cover (but this difference could not, without habitat selection, account for the replacement of the Meadow Pipit by the Willow Warbler in the young fir plantations of the Breckland). Between yet more remotely related forms specialisation may be so marked as to prevent in itself any overlap of habitat. As one would expect, differential specialisation tends to increase the longer the forms have been separated.

A serious objection to this view is the apparent absence of species in the making through differential habitat selection. Nor does it seem likely that these have been overlooked. The case of the Cuckoos (Baker, 1923; Jourdain, 1925), which seem to be splitting into races with different host preferences, is scarcely comparable. In the case of geographical isolation among birds there are many sub-specific forms which illustrate the intermediate stages of the process. It may be noted in passing that geographical isolation is in birds rarely produced through an impassable physical barrier, but usually through a psychological factor, the habit so strongly developed in many forms of returning to breed where they were reared in the previous year. Thus one

geographical race will not infrequently pass regularly on migration through the region where an allied race breeds. In this respect it is comparable to the postulated isolation by habitat selection.

To conclude, the view advanced here that specific divergence has at times been achieved through habitat selection is admittedly hypothetical. There is some evidence to favour it, and there are some objections (probably not insurmountable). Until there are more data one cannot prove or disprove it. It was included primarily to show that considerations of evolution and the species problem do not invalidate the habitat-selection hypothesis, which has been formulated to explain present-day distribution. The discussions on the species problem by Richards and Robson (1926), Robson (1928), also Fisher (1931) are of interest with regard to these views concerning birds.

(7) *Final note on animal distribution.*

The main object of this paper was to show the importance of the psychological factor in limiting bird distribution. Birds, as a group, are well adapted to a terrestrial environment and can withstand great variation in the climatic conditions. At the same time they have well-developed powers of flight, and hence there are few barriers to their dispersal. In spite of this almost all species of birds have a comparatively restricted breeding range. The reason is apparent from this paper, and is to be found in the possession by the bird of the instinct to select its own breeding ground. This instinct tends to restrict an animal to the locality, and to the type of locality, where its parents proved successful, which promotes segregation, both geographical and of habitat, with the result that species are differentiated, each with a restricted distribution.

As remarked by Thompson and Parker (1927), there are many cases where the distribution of an animal has been shown to be limited by some simple factor, such as temperature or moisture, in some instances quantitatively as well as qualitatively; but even though some biological phenomena are reducible to definite and constant combinations of certain physico-chemical causes, it is not necessary, or indeed probable, that all should be. This is borne out by their conclusion that the cause of behaviour in host selection by an entomophagous parasite is on a psychological plane, and this paper presents a similar conclusion with regard to the distribution of birds.

SUMMARY.

1. The Breckland heaths have been planted with young pines. Until the trees are some four years old only heathland birds occur, but within the next five years these die out, being replaced by a new avifauna.

2. Deficiency of nesting sites explained a few distributions.

3. Food, though clearly important in controlling the total bird population, did not appear to limit the distribution of any species investigated.

4. Most distribution could be explained only by postulating the existence of specific habitat selection—that each species selects its ancestral habitat, instinctively recognising it by the conspicuous, not necessarily the essential, features. The evidence for this is summarised at the end of Part II (see p. 254).

5. Although it restricts distribution, habitat selection ensures a suitable habitat, replacing the chance dispersal of other animals.

6. Birds rarely break away from the ancestral habitat[1], at times successfully.

7. Passerine species of the North Temperate region often tend to occupy distinct but adjoining habitats, affording the same essential requirements but differing in their conspicuous features. No correlated adaptations are apparent, and it is tentatively suggested that in such species segregation has been achieved with the assistance of differential habitat selection.

8. The paper emphasises the importance of the psychological factor, usually ignored, in bird distribution.

[1] See foot-note, p. 255.

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APPENDIX I. 1931 COUNTS.

Type of vegetation	Locality	Stock Dove	Lapwing	Stone Curlew	Wheatear	Skylark	Meadow Pipit	Whinchat	Stonechat	Willow Warbler	Whitethroat	Wren	Dunnock	Blackbird	Goldcrest	Chaffinch	Common Partridge	Red-legged Partridge	Pheasant	Yellow Bunting	Other species
Grass turf	Little Heath (nr. Larling)	2	3	7	18	13	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1 Wood Lark
Thin grass	Lakenheath Warren	1	3	3	3	52	17	.	1	.	.	.	.	.	.	.	.	.	.	.	
Thin grass and thin bracken	Lakenheath Warren	.	1	1	.	30	11	1	3	.	.	2	.	.	.	.	2	.	.	.	
Grass and thick bracken	Brettenham Heath	.	.	.	.	47	8	20	9	.	2	2	.	.	.	.	.	.	.	.	1 Tree Pipit / 1 Reed Bunting
Heather and thin bracken*	Roudham and Bridgeham Heath	.	.	4	.	38	46	14	.	.	.	.	.	.	.	.	3	1	3	1	5 Yellow Wagtail / 1 Cuckoo
P. 27. Poor	Thetford Warren	.	.	.	.	39	23	4	3	.	.	.	.	.	.	.	2	4	.	.	
P. 27. Good	Bromehill	.	.	1	1	6	5	13	2	6	.	.	.	.	.	.	.	2	.	3	1 Wood Lark
P. 26. Poor	Wangford Warren	.	.	.	.	46	44	10	.	11	.	.	.	.	.	.	.	.	2	1	1 Tree Pipit / 2 Yellow Wagtail
P. 26. Good	West Tofts Heath	.	.	.	.	6	7	8	1	3	2	1	.	.	.	.	1	.	2	.	1 Yellow Wagtail
P. 25. Poor†	Warren Wood	.	.	1	.	33	16	5	3	15	.	3	.	.	.	.	.	.	2	.	1 Yellow Wagtail
P. 25. Fair	Elvedon Warren and Thetford-Elvedon Road	.	.	1	.	14	8	3	1	17	2	4	.	.	.	.	1	2	5	2	1 Yellow Wagtail / 1 Grasshopper Warbler / 1 Tree Pipit, 2 Nightjar
P. 24. Fair	Wangford Warren	.	.	.	.	6	4	3	1	27	4	3	2	3	.	.	.	.	2	.	2 Yellow Wagtail / 2 Lesser Redpoll f.‡
P. 24. Good	Parsonage Heath and Warren Wood	.	.	.	.	5	1	.	2	29	7	7	6	.	1	.	.	.	1	2	1 Lesser Redpoll f. / 1 Coal Tit family f.
P. 23. Good	Parsonage Heath	.	.	.	.	.	2	2	.	38	10	2	2	.	1	4	.	.	.	.	1 Robin / 1 Marsh Tit family f.
P. 22. Very fair	Wangford Warren	.	.	.	.	.	1	.	.	.	2	2	5	7	3	.	.	.	3	6§	1 Linnet ? f. / 5 Lesser Redpoll ? f.

* Omitted from Table II, as much like "Thin grass with thin bracken."
† Omitted from Table II, as much like "P. 26. Poor."
†† "f." indicates feeding only.
§ Near edge.

APPENDIX II. 1933 COUNTS.

Type of vegetation	Locality	Skylark	Meadow Pipit	Whinchat	Stonechat	Willow Warbler	Whitethroat	Wren	Dunnock	Blackbird	Goldcrest	Chaffinch	Song Thrush	Pheasant	Yellow Bunting	Other species
P. 27. Poor	Thetford Warren	13	19	3	·	7	·	·	ʼ	·	·	·	·	·	·	
P. 27. Good	Bromehill	2	1	2	·	10	·	1	1	2	·	·	·	1	1	1 Linnet f.* / 1 Lesser Redpoll ? f.
P. 26. Poor	Wangford Warren	9	4	1	·	17	4	2	·	·	·	·	·	·	·	1 Red-legged Partridge
P. 26. Good	West Tofts Heath	·	·	3	·	21	1	3	2	3	·	2	1	·	1†	2 Linnet / 1 Lesser Redpoll ? f.
P. 25. Fair	Elvedon Warren and Thetford-Elvedon Road	11	2	8	·	37	10	3	10	10	·	2	1	3	3	1 Nightjar
P. 24. Fair	Wangford Warren	1	·	·	·	22	5	3	·	4	1	1	·	·	·	
P. 24. Good	Parsonage Heath and Warren Wood	·	·	·	1	53	7	16	10	12	1	23	5	2	4	1 Sedge Warbler / 1 Coal Tit f.
P. 23. Good	Parsonage Heath	·	·	·	·	35	5	16	6	13	2	17	11	3	4	3 Lesser Redpoll f.
P. 22. Very fair	Wangford Warren	·	·	·	·	35	·	13	14	8	6	12	4	1	2	1 Sedge Warbler / 1 Turtle Dove ? f. / 1 Coal Tit f.

Number of breeding pairs of

* "f." indicates feeding only. † At edge.

APPENDIX III. SPECIES MENTIONED IN THE TEXT.

1. Lesser Redpoll — *Carduelis linaria cabaret* P. L. S. Müll.
2. Linnet — *Carduelis c. cannabina* (L.)
3. Common Crossbill — *Loxia c. curvirostra* L.
4. Chaffinch — *Fringilla c. coelebs* L.
5. Yellow Bunting or Yellow Hammer — *Emberiza c. citrinella* L.
6. Reed Bunting — *Emberiza s. schoeniclus* (L.)
7. Wood Lark — *Lullula a. arborea* (L.)
8. Skylark — *Alauda a. arvensis* L.
9. Tree Pipit — *Anthus t. trivialis* (L.)
10. Meadow Pipit — *Anthus pratensis* (L.)
11. Rock Pipit — *Anthus spinoletta petrosus* (Mont.)
12. Yellow Wagtail — *Motacilla flava rayi* (Bp.)
13. Coal Tit — *Parus ater britannicus* Sharpe and Dresser
14. Marsh Tit — *Parus palustris dresseri* Stejn.
15. Goldcrest — *Regulus regulus anglorum* Hart.
16. Chiffchaff — *Phylloscopus c. collybita* (Vieill.)
17. Willow Warbler — *Phylloscopus t. trochilus* (L.)
18. Sedge Warbler — *Acrocephalus schoenobaenus* (L.)
19. Whitethroat — *Sylvia c. communis* Lath.
20. Mistle Thrush — *Turdus v. viscivorus* L.
21. Song Thrush — *Turdus philomelus clarkei* Hart.
22. Blackbird — *Turdus m. merula* L.
23. Wheatear — *Oenanthe oe. oenanthe* (L.)
24. Whinchat — *Saxicola r. rubetra* (L.)
25. Stonechat — *Saxicola torquata hibernans* (Hart.)
26. Robin — *Erithacus rubecula melophilus* Hart.
27. Dunnock or Hedge Sparrow — *Prunella modularis occidentalis* (Hart.)
28. Wren — *Troglodytes t. troglodytes* (L.)
29. House Martin — *Delichon u. urbica* (L.)
30. Nightjar — *Caprimulgus e. europaeus* L.
31. Green Woodpecker — *Picus viridis virescens* (Brehm)
32. Cuckoo — *Cuculus c. canorus* L.
33. Stock Dove — *Columba oenas* L.
34. Stone Curlew — *Burhinus oe. oedicnemus* (L.)
35. Ringed Plover — *Charadrius h. hiaticula* L.
36. Lapwing — *Vanellus vanellus* (L.)
37. Great Bustard — *Otis t. tarda* L.
38. Pheasant — *Phasianus colchicus* L.
39. Common Partridge — *Perdix p. perdix* (L.)
40. Red-legged Partridge — *Alectoris r. rufa* (L.)

DIFFERENTIAL BEHAVIOUR OF *LUCILIA SERICATA* MEIG. AND *LUCILIA CAESAR* L. IN NATURAL ENVIRONMENTS

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In the course of studies on the European blowfly, *Lucilia sericata* Meig. (Holdaway, **1**), at Toulouse, France, the writer observed that early in June on sunny days fly traps caught a high proportion of *L. sericata*, while on dull days they caught a high proportion of *L. caesar* Linn. Under the name *L. caesar* in this paper *L. ampulacea* Vill. should also be included, for at the time these observations were made females of the two species were indistinguishable and other observations demonstrated that the two species were active under similar conditions. The relative proportion of males of the two species captured indicated that *L. caesar* was the more abundant to the extent of about six to one.

The traps used were small spherical gauze traps, such as are in common use in Great Britain, and were baited with small pieces of meat. In the absence of records of the number of hours of sunshine, mean nebulosity readings were used to compare conditions of sunlight on succeeding days. The nebulosity readings were from official records made three times a day at 7 a.m., 1 p.m. and 6 p.m. and were obtained through the courtesy of Prof. Nicholas, Professor of Agriculture at the University of Toulouse.

The records given in Table I were obtained from traps set in the University garden. The traps were subject to a certain amount of shade and, since nebulosity readings taken only three times a day cannot give a particularly good measure of conditions of sunshine, the figures can only be taken to be suggestive of differential behaviour of the two species of flies. The sex of the flies caught was recorded. However, since the majority of the flies caught were females and there was apparently no difference as regards reaction to light of the two sexes in each species, for simplification of the tables the sexes have not been tabulated separately.

Table I. *Records of flies caught from June 5th–10th inclusive.*

Date	5	6	7	8	9	10
L. sericata	8	1	58	67	16	5
L. caesar group	24	4	21	41	25	13
L. sericata (%)	25	20	73	62	39	28
L. caesar group (%)	75	80	27	38	61	72
Mean nebulosity	9	9·6	5	5·2	9·4	10

Where nebulosity 0 = clear sky; 10 = overcast.

In order to study further the differential behaviour of the two species an experiment was set up in which three similar traps each baited with 10 gm. of fresh mutton were placed, one in complete shade and the other two in open sunlight 10 yards apart and 100 yards from the shade trap. The number of flies caught in these traps is given in Tables II and III.

Table II. *Records of flies caught June 19th–24th inclusive.*

Date	19	20	21	22	23	24	Total
A. Shade:							
L. sericata	0	0	0	1	0	0	1
L. caesar	1	60	5	90	7	49	212
B. Sun:							
L. sericata	3	1	68	23	Trap stolen		95
L. caesar	0	0	0	1	Trap stolen		1
C. Sun:							
L. sericata	5	6	25	Trap damaged		12	48
L. caesar	1	0	1	Trap damaged		0	2
Mean of B and C Sun:							
L. sericata	4	4	47	23	—	12	90
L. caesar	0·5	0	0·5	1	—	0	2

Table III. *Summary of data in Table II.*

Date	19	20	21	22	23	24
A. Shade:						
L. sericata (%)	0	0	0	1	0	0
L. caesar (%)	100	100	100	99	100	100
Mean of B and C Sun:						
L. sericata (%)	89	100	98	97	—	100
L. caesar (%)	11	0	2	3	—	0
L. sericata captured per day (%):						
Shade	0	0	0	4	0	0
Sun	100	100	100	96	—	100
L. caesar captured per day (%):						
Shade	66	100	91	99	100	100
Sun	34	0	9	1	0	0

The results of this experiment show that *L. sericata* is active in open habitats while *L. caesar* is active in shady habitats, and confirm the original suggestion that their reactions to environmental conditions are different.

In Table IV the percentage of *L. sericata* and *L. caesar* caught in the sun traps is given together with the mean daily nebulosity for the period of the experiment. It will be seen that the relationship between the percentage of each species caught and the mean nebulosity is not evident in this experiment as it was in the earlier observations. The nebulosities recorded were on the whole lower than those recorded during the earlier observations while the daily temperatures, given in Table V, were higher. The evidence suggests that during moderate temperatures nebulosity records give a measure of the differential behaviour of the two species but that at higher temperatures the relationship if present is not the same. Possibly at very high nebulosities a relationship may be evident.

Table IV. *Percentage of* L. sericata *and* L. caesar *caught in sun traps, together with mean nebulosity for the day.*

Date	19	20	21	22	23	24
L. sericata	89	100	98	97	—	100
L. caesar	11	0	2	3	—	0
Mean nebulosity	4	4·3	6·6	3·3	—	1·3

Table V. *Daily temperatures in degrees centigrade, at Toulouse, June 5th–10th and June 19th–24th—the periods of the observations.*

Date	7 a.m.	1 p.m.	6 p.m.	Daily mean	Period mean
5	16·4	20·0	19·5	18·6	
6	17·1	22·5	21·8	20·5	
7	18·6	26·0	27·0	23·9	20·6
8	19·2	23·8	22·3	21·8	
9	17·0	19·3	18·1	18·1	
10	17·3	21·2	22·1	20·2	
19	20·6	29·8	21·7	24·0	
20	19·6	28·0	25·4	24·3	
21	18·6	24·6	26·1	23·1	23·4
22	17·8	24·5	23·8	22·0	
23	16·9	25·2	25·0	22·4	
24	19·3	27·3	27·2	24·6	

It is impossible to decide on the evidence available whether the differential behaviour of the two species was due to differences in light intensity or to differences in intensity of heat, or to a combination of both factors. What seems probable is that the range of waves of radiant energy favouring activity of *L. sericata* is higher than the range for *L. caesar*; that when the environmental conditions are moderate *L. caesar* will frequent, under conditions of high nebulosity, open environments, but with the advance of summer even a relatively high nebulosity is insufficient to lower the radiant energy sufficiently in open environments to a range favourable to *L. caesar*.

ACKNOWLEDGMENTS.

SUMMARY.

From trap records it has been found that *L. sericata* Meig. frequents open habitats and *L. caesar* Linn. shady habitats. A comparison of records from traps in open situations with records of nebulosity and temperature suggests that the range of waves of radiant energy favouring activity of *L. sericata* is higher than that favouring activity of *L. caesar*.

REFERENCE.

(1) **Holdaway, F. G.** (**1930**). "Field populations and natural control of *Lucilia sericata*." Nature, 126, 648–9.

ON THE INFLUENCE OF THE RATE OF FLOW ON THE FISH FAUNA OF THE RIVERS OF CENTRAL ASIA

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(*With seven Figures in the Text.*)

A NUMBER of scientists (Van dem Borne, Severtzov, Ellis, Hesse) have been studying the influence of the rate of flow on the distribution of fishes in rivers and have attempted to divide the rivers into groups according to the species of fish found in them. As regards fishes of Central Asiatic rivers with very high rates of flow, the latter must influence the qualitative as well as the quantitative composition of the communities, and the sharp transition from flowing to stagnant water in Central Asia gives a favourable opportunity of tracing such variations in the composition of the fish communities in the whole course of the river.

My material has been obtained by analysing test catches and comparing the results obtained with physico-geographical data. After having obtained the percentage of each species in the catch, I assigned these data to the special points where the fishing took place, and I then compared the fluctuations in percentage curves with the modifications in hydrological or hydrobiological conditions. Such investigations were carried out in three rivers: Chu (from Vassilievka to Sopar-Kusha, 1929), Nura (from Ak-Mola to the lake Kurgoljin, 1930) and Amu-Darja (from Charjui to Kanta-Uzekm, 1931).

These three rivers differ considerably: the river Chu in its upper and middle courses, as well as the Amu-Darja, carry a large amount of suspended matter and have a very swift current; both rivers then become rushy; the Amu-Darja, after passing through these rushes, discharges into the Aral sea, whereas the Chu, having lost itself among the rushes, becomes in summer in the lower part of its course a succession of pools, connected with each other only in spring. Therefore the flooded area between Guliaevka and Alexeyevka as regards the distribution of the fish fauna may be considered nowadays the delta of the river Chu. The river Nura differs strongly from the others. In the first place it has not so swift a current as the Chu and the Amu-Darja. Its waters throughout its whole course are clearer, except in a few places, and its depth at certain places is very considerable. In the lower part of its course the Nura passes through a series of lakes and falls into lake Kurgoljin without forming any delta. It is quite natural that in such rivers as the Chu and the Amu-Darja with a course flowing through about 6° (Amu) we find fishes with

entirely different ecology. The hydrological conditions which have an immediate influence on the fish population also affect the other organisms in the river, both animal and plant life, and in that way have an indirect bearing on the fishes that are found in the river. P. I. Usachev (**24**) points out in his work on the phytoplankton of the river Yenisei that from Krasnoyarsk (where the river is a typical mountain stream) the following changes in the phytoplankton are to be observed: the productivity of the plankton increases in the lower course and the number of species increases also on account of forms growing in slowly running waters.

The rate of the flow also exercises a strong influence on the zoo-plankton. Miroshnitchenko (**17**) concludes from his investigations of the zoo-plankton of the Dniepr rapids that "the influence of the rapids on the quantity of the zoo-plankton is obviously negative." Usually two sections of a river which are contiguous, but differ as to the rate of flow, have a different plankton not only in quantity, but in quality (**16**). The lower course of rivers is characterised by the abundance and character of the plankton.

Naturally the distribution of the plankton affects the distribution of fishes. The fry accumulate in regions where the plankton is most abundant— the deltas and lower portions of rivers (**8**). However, the abundance of the plankton cannot always offset the negative effect of other conditions. For instance, the fry of *Pelecus cultratus* (L.), which feed almost exclusively on plankton (**23**) in the Amu-Darja, prefer the river-bed to the lakes, although owing to the absence of plankton in the river they are obliged to feed on other food (see below, Table I); they are also found in lakes, but much more seldom.

Table I. *Distribution of* Pelecus cultratus (*L.*) *in the bed and lakes of the river Amu-Darja.*

	Lakes of the left bank	Bed of the river, including backwaters	Lakes of the right bank
Pelecus cultratus in catch (%)	1	9·25	3·7
Amount of plankton	Much	Absent	Much

In the benthos we find also modifications from the upper to the lower course of the river. Martynov (**15**) on the basis of the different ecology of the larvae of *Trichoptera* suggests classifying them into groups according to their occurrence in different parts of the stream. In the samples from our catches on the Amu-Darja, there is, in spite of chance variations, a general increase in productivity from the upper to the lower regions. In general a very low productivity of the stream was noted, and an increase of productivity in places with a slower current.

The river-distribution of fish in Turkestan rivers may be divided according to the fish population into three groups: rivers which discharge into seas and have *anadromous* fishes; rivers that formerly discharged into seas, but

which now lose themselves in the steppe; and rivers that flow into lakes. These three groups differ according to the distance the roophile forms descend toward the mouth of the river, and the limnadophile forms ascend the river.

The ecology of migratory fishes, which, when adult, enter the river for a short time only to spawn and then return to the sea, cannot be studied by the present method. With regard to the fry we have quite another situation. It is true that the fry of sturgeon (*Acipenser nudiventris* Lov.), found in the Amu-Darja in rather insignificant numbers, can be estimated with difficulty, but the application of this method in investigations of the distribution of the fry of barbels (*Barbus*) affords some data. Unfortunately during my work I had no apparatus for measuring the rate of flow, and therefore I had to make use of indirect indications, e.g. of the quantity of suspended particles in a litre of water (raw sediment in cm. for 1 litre) and the transparence of the water determined by means of the Secchi disk. In order to determine the effect of the rate of flow on the Amu-Darja barbels (two species), I used the percentages for these species in the lakes of the right and left banks of the Amu-Darja and in its bed.

Table II. *Distribution of the fry of the Aral barbel* (Barbus brachycephalus) *and of the Turkestan barbel* (Barbus capito) *in the bed and lakes of the Amu-Darja.*

	Lakes of the left bank	Bed of the river	Lakes of the right bank
B. brachycephalus (%)	37·5	94·8	22·2
B. capito (%)	62·5	5·2	77·8

In studying the figures obtained we see that the ecology of these two species is very different: while the Aral barbel is a typical roophile and less commonly enters the lakes, the Turkestan barbel, sometimes found in the bed, prefers the lakes, where it spawns. In order to verify the data obtained I tried to determine the percentage of barbels in the river Chu, where both species are also found, though *B. brachycephalus* is rare. In the bed of the Chu it is only 17 per cent. of *B. capito*. In the whole course of the river the percentage of the latter much exceeds that of *B. brachycephalus*. The percentage of *B. brachycephalus* exceeds considerably that of *B. capito* in only two parts of the river: where the Chu digs its way through the spurs of the Kurdai and forms rocky banks, and at a distance of 80–90 km. below Novotroitzkoe, where there are large rapids on a sandstone bed. Here *B. brachycephalus* amounts to 70 per cent. Thus, after analysing the data, we conclude that the Aral barbel (at any rate, when sexually immature) is a typical roophile. If we consider its distribution in Amu-Darja we shall find a uniform distribution throughout the whole portion of the river investigated, the fry keeping chiefly in the shallows.

I proceed now to analyse the curves of fishes living in the river itself (see Table III). Let us take the river Chu as the most convenient for such an analysis. We observe here two different groups of curves, at first forms which reach a

Table III. *Percentage of some species of fishes caught at stations along the river Chu.*

No. of station	Place of catch	Limpidity	Total amount	*Schizothorax pseudaksaiensis* %	*Leuciscus leuciscus* %	*Capoetobrama kuschakewitschi* %	*Rutilus rutilus* %	*Leuciscus idus* %	*Abramis brama* %	Other species %
1	25 km. below the village Vassilievka	Turbid water carrying many suspended particles of sand and slime	120	14	36	18	—	—	—	32
2	Ak-bashi farm	Do.	80	6	50	44	—	—	—	—
3	15 km. below Uspenovka	Do.	110	14	45	41	—	—	—	—
4	—	Do.	100	10	40	50	—	—	—	—
5	20 km. below Blagovestchenskoe	Current somewhat slower, water more limpid, deposits less	112	3	33	23	—	—	—	41
6	27 km. below Blagovestchenskoe	Turbid water carrying much sand and slime	160	2	56	30	—	—	—	12
7	35 km. above Novotroitzkoe	Very turbid water, much suspended sand	90	2	25	38	12	—	—	23
8	2 km. above village Vosnesenovka	Turbid water	70	2	50	14	29	—	—	5
9	Village Novotroitzkoe	Do.	174	2	17	15	26	—	—	40
10	15 km. below village Novotroitzkoe	Do.	65	—	46	38	12	—	—	4
11	—	Do.	112	—	36	13	18	—	—	33
12	6 km. below Alexeyevskoye (5th)	Water somewhat more limpid than above	117	—	30	26	15	2	—	27
13	55 km. below Novotroitzkoe	Do.	97	—	2	46	19	10	7	16
14	7 km. below Iliynskoye (6–12th)	Turbid water	140	—	11	55	4	22	3	5
15	35 km. above Guliaevka	Very turbid water	125	—	—	60	—	—	—	40
16	20 km. above Guliaevka	Turbid water	145	—	8	34	23	3	1	31
17	Guliaevka (inundated area near Guliaevka)	In some channels limpid, in others turbid	79	—	9	30	9	9	2	41
21	Bazaba settlement	Almost limpid	112	—	—	—	27	9	4	60
22	River Chu, near the lake Little Kamkaly	Limpid	67	—	—	—	37	27	3	33
23	Kazykty settlement	Do.	125	—	—	—	21	3	9	67
24	Karassu, 7 km. above Lambel	Do.	100	—	—	—	40	20	20	20
27	Kchiyly settlement	Limpid, slightly troubled, near watering-places for cattle	100	—	—	—	83	2	10	5
28	Itmurun settlement	Limpid	95	—	—	—	18	29	53	—
29	Ku-Aral settlement	Do.	315	—	—	—	10	6	3	81
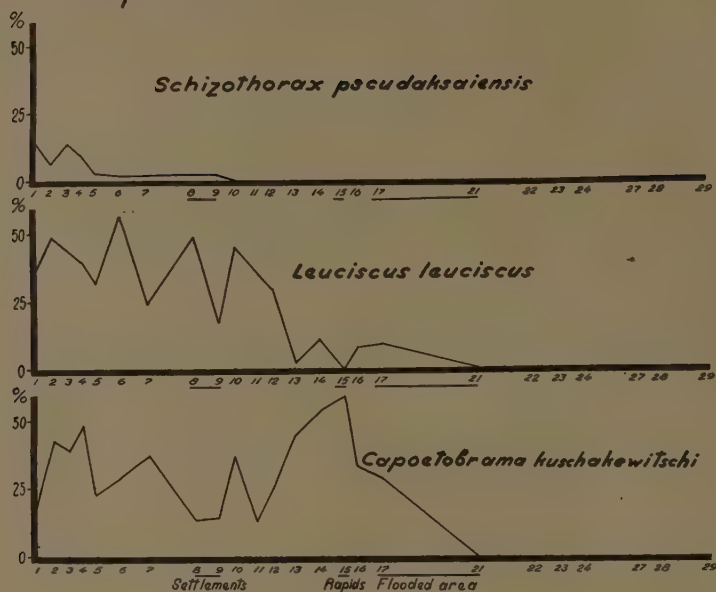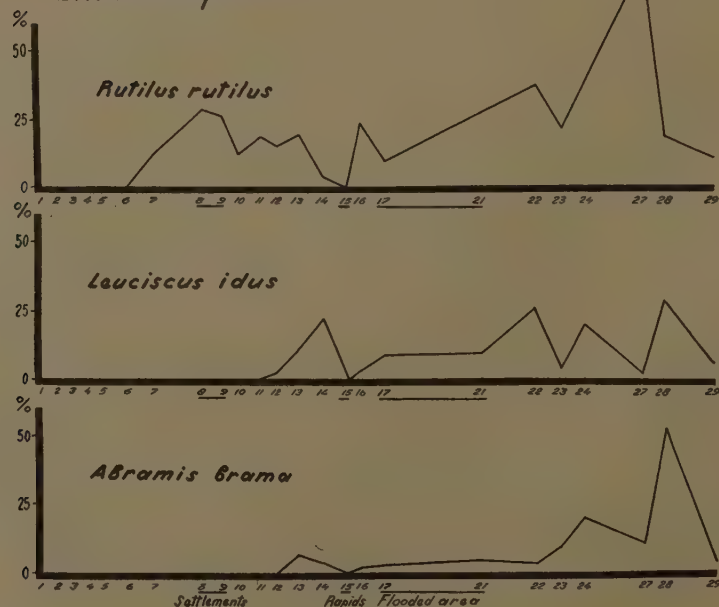
Fig. 1. Distribution curve of roophiles and limnadophiles (percentages in catches) in the river Chu.

maximum in the middle course of the river as far as the "delta" (the flooded area near Guliaevka). Among those forms we find *Schizothorax pseudaksasiensis*, *Capoetobrama kuschakewitschi* (Kessl.), *Leuciscus leuciscus* (L.) and *Diplophysa dorsalis* (Kessl.). In analysing the curves we may notice the following: a drop in the curves of these roophile species at Station 5 (in the region of the village Blagovestchenskoe) and a sharp rise at Station 6.

If we consider the character of the river, we find that at Station 5 the current has slowed down and has overflowed a considerable area; the bottom of the creeks and backwaters is covered with a thin layer of slime and the water has become clearer. At Station 6 the Chu digs its way through the
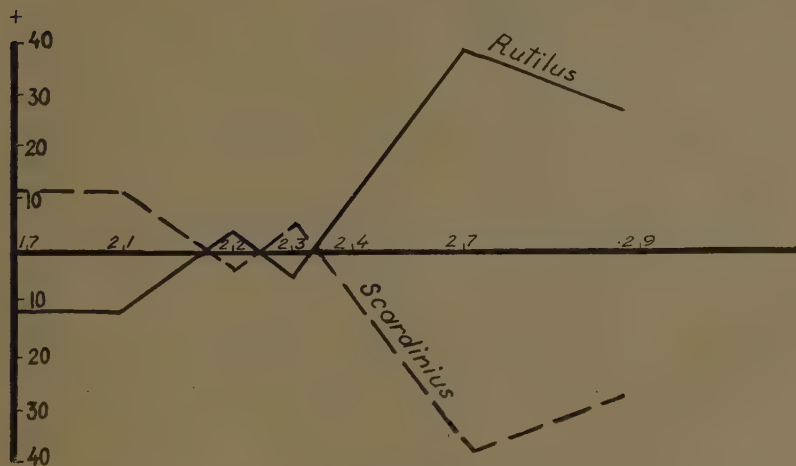
Fig. 2. Relation of *Rutilus rutilus* to *Scardinius erythrophthalmus* in the lower course of the river Chu.

spurs of the Kurdai and becomes a swift torrent carrying a large amount of suspended particles; we naturally find here a large percentage of roophiles. Further down we note a drop in the curves of roophiles (*Cobitidae* disappear altogether) at Stations 8 and 9, in the region of the villages of Vosnesenovka and Novotroitzkoe where the river flows more slowly. The limnadophiles (*Rutilus*, *Skardinius*) appear here in considerable numbers. Further on at Station 15 (rapids) the curves show that the limnadophiles (*Rutilus*, *Skardinius*) are replaced once more by roophiles which had previously almost disappeared. Down the river the limnadophiles increase more and more, whereas the roophiles disappear completely at Station 21 (Bazaba); in the lower course of the river in the semi-stagnant waters the limnadophiles preponderate. But among these, several groups are differently affected by the stagnancy of the water. In the lower portion of its course the Chu has a current only in spring;

later on it dries up gradually and its water forms pools in the bed of the river, which becomes salty, beginning with the lowest pools. Some of these pools, which are fed by springs, remain fresh almost the whole summer, but they are an exception. In order to show the different relations of the fish in the lower part of the river to stagnant water, give the percentage of *Scardinius erythrophthalmus* (L.) and *Rutilus rutilus* (L.) in the catches in the lower course of the Chu. I have taken a ratio of 1:1 as a norm, increases being indicated by a + (plus) and a decrease by a − (minus). Comparing these percentages with the changes of the water in different basins (Kara-Su), we can discover some regularity: thus at Stations 22, 24, 27 and 29 the water has a perceptible mineral content, and has a bitter salt flavour. The water in the basin at Station 29 (Ku-Aral) has the lowest mineralisation, and here the percentage of *Scardinius erythrophthalmus* increases. At Stations 17, 21 and 23 the water is slightly mineralised, though imperceptibly to the palate. The curve of the *Scardinius* has negative indices for all basins which are strongly mineralised and rises in fresh-water basins. Thus, among the fishes of Turkestan and even in the group of limnadophiles, one observes a number of sub-groups reacting in a different way to stagnant water. In rivers of the type of the Amu-Darja, where a high rate of flow and turbid water are maintained all the way to the lower part of their course, the distribution of the fish is naturally quite different. In the main river we do not find any limnadophiles; they take refuge in the branches, lakes and deeps of the delta, whereas in the bed they appear only occasionally. In the curves of roophiles in the investigated portion of the Amu-Darja no considerable fluctuations are observable, and a gradual decrease begins only at the upper delta (Tash-Saka); but even in the branches of the lower delta (Kartabay, Model) these forms are encountered in large numbers, according to M. I. Markoon[1]. The decrease in the number of roophiles in the Amu-Darja does not include the limnadophiles, as it does in the Chu, but it does include the roobiontes (e.g. *Aspius aspius*).

Table IV. *Distribution of fish in the middle course of the Amu-Darja.*

Station	Clearness	Sediment c.c.	*Capoeto-brama kuscha-kewitschi* %	*Aspio-lucius esocinus* %	*Silurus glanis* %	*Barbus brachy-cephalus* %	Other species %
Charjui	0	28	26	3	2	53	16
Kash	0	26	61	11	2	7	19
Djiguit-Kaba	0	25	44	0	9	29	18
Dargan-Ata	0	30	85	5	1	8	1
Tash-Saka	0	22	53	25	1	15	6
Shabaz-Tugai	1·5	24	44	11	11	22	12
Nukus	2	22	19	2	8	7	64

An altogether different condition may be observed in the river Nura. As I have already stated, this river, being for almost its whole course a steppe-river, has not a high rate of flow and its waters are much clearer. As a

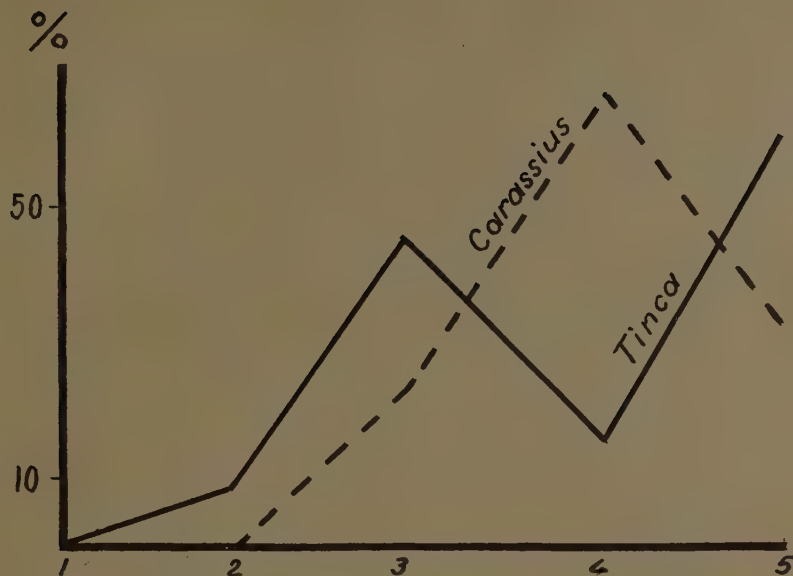[1] Personal communication.

Fig. 3. Distribution curves of limnadophiles in the river Nura.

Fig. 4. Distribution curves of roophiles and limnadophiles at four points of the flooded area of the river Chu at Station 17.

Table V. *Percentages of different species of fishes caught at four places of the river Chu where it divides into arms near the village of Guliayevka.*

No. of fishery	Place where caught	Nature of bottom	Plant	Current	Limpidity	*Capoetobrama kuschakewitschi* %	*Leuciscus leuciscus* %	*Silurus glanis* %	*Cyprinus carpio* %	*Aspius aspius* %	*Scardinius erythrophthalmus* %
1	Guliaevka channel close to its separation from the Kok-Uzek	Sand; here and there boulders of sandstone	None	Very swift	Turbid, brown-yellow	63	20	14	1	—	—
2	Beginning of Kok-Uzek before it enters the bulrushes	Sand	None	Swift	Turbid, whitish-yellow	51	10	16	3	13	3
3	Branch of the Kok-Uzek, to the right at the beginnings of the bulrushes	Sand with a thin layer of slime	*Phragmites* on the shores	Slower	Nearly transparent	8	5	3	9	22	13
4	Blind end of one of the right arms of the Kok-Uzek	Slimy	Shore covered with *Phragmites*; in the water *Briotomus* (near the shore), pondweeds and hairweeds	Almost no current	Transparent	—	2	1	7	34	24

consequence many species of limnadophiles are found very far up the course of the Nura and are fairly numerous. I give below the curves in the percentages of *Carassius carassius* (L.) and of *Tinca tinca* (L.) in the Nura. Evidently these fish cannot travel far up the river unless the current is slow. In comparing these curves with the electro-conductivity of the water (by P. I. Usachev (24[1])) we note an abrupt change in the curve of *Carassius carassius* (L.) in the region of lake Byrtaban, due to the greater stagnation of the water (electro-conductivity exceeding 1000). In other words here, as in the Chu, the limnadophiles react differently to the mineralisation of the water. Whilst *Tinca tinca* (L.) outnumbers *Carassius carassius* (L.), where the mineralisation is less than one thousand, in places where it exceeds this figure we find *Carassius carassius* (L.) predominating.

Table VI. *Distribution of the limnadophiles in the river Nura.*

Station	*Tinca tinca* (L.) %	*Carassius carassius* (L.) %	Other species %	Electro-conductivity
1. Ak-mola	—	—	100	No data
2. Nura, lower than Urozak	9	—	91	No data
3. Intel, between lake Diany-Bek and Ujaly	45·7	23·7	30·6	854·4
4. Lake Byrtaban	14·8	66·6	18·6	1284·3
5. Saga	60	33·3	6·7	973·5

I have also explored two "deltas," namely the lower delta of the Amu-Darja and the overflowed areas and deeps of the Chu near Guliaevka, which may be considered as deltas, as I have already said (see Tables V and VI). At the time of our survey (in 1929) the Chu in the Guliaevka region discharged through three main channels. The largest and swiftest is to the left near Guliaevka: the water is turbid. In the middle is the Kok-Uzek: Kok-Uzek is overgrown with rushes and has not so swift a current as the Guliaevka channel. Finally we find the blind arm Kara-Uzek. The "delta" of the Chu has the swiftest rate of flow in its left channel; the farther to the right the less is the rate and the more limpid and stagnant the water. The Amu-Darja delta during our survey had the largest amount of water in the middle channel, whilst to the left and to the right "uzeks" (i.e. canals) branched off, ending in blind arms. In conformity with such arrangement of the branches the distribution of the fish fauna varies. In the Chu the roophiles attain the maximum in the left of Guliaevka channel and decrease gradually towards the right, giving way to limnadophiles. In the Amu-Darja (I give data concerning the lakes of the central and peripheral portions of the delta), the roophiles and the roobiontes *Cyprinus carpio* (L.)[2] are at a maximum (roophiles only being

[1] *In litt.*
[2] To which group the carp belongs is so far open to question; tentatively I place it among the roobiontes, since it travels far up the rivers and is found in the main channel in large numbers;

found) in the central part of the delta, and are replaced by limnadophiles (native bream and *Carassius*) on the borders.

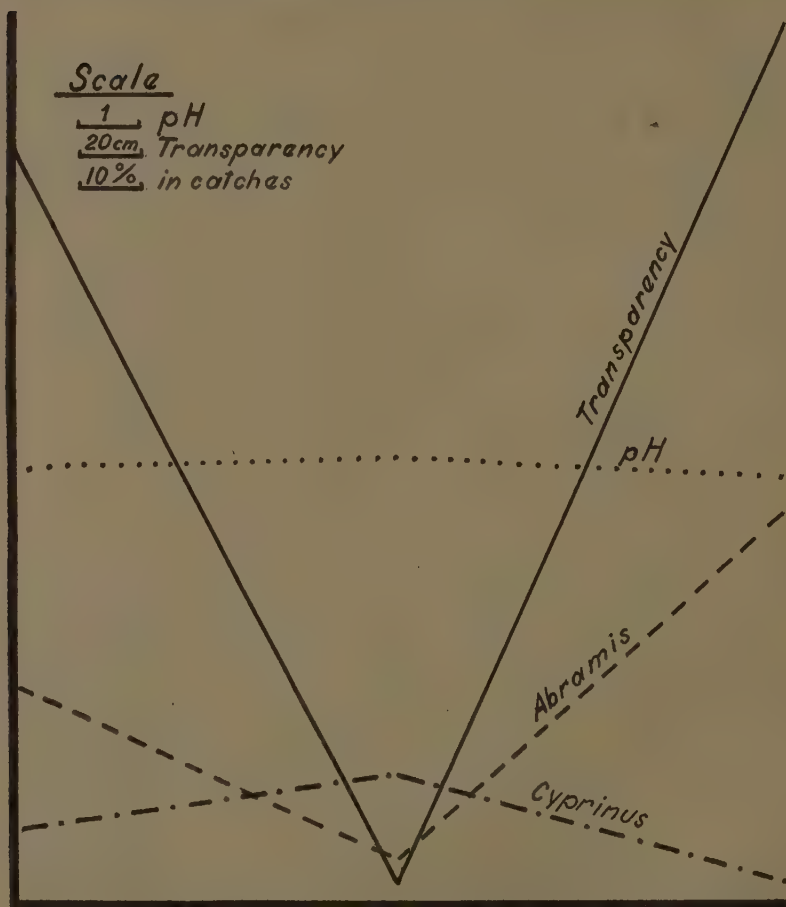Some regular phenomena are likewise to be noticed in the delta system of

Fig. 5. Distribution curves of the transparency, of *pH* and of percentages in catches of *Abramis brama* and *Cyprinus carpio* in the "delta" of the Amu-Darja.

rivers, in their backwaters and deeps. I have already outlined the types of backwaters in the river Chu and the distribution of fishes in them. Something of the same sort may be observed in the Amu-Darja. As an example I quote

the rate of flow does not affect it. On the other hand it gathers deep in the backwaters (see below, p. 277), the presence of suitable food being apparently the cause. At any rate the carp avoids stagnant water.

the distribution of the carp and of the *Capoetobrama kuschakewitschi* in one of the backwaters of the Amu-Darja investigated by us. The distribution of *Capoetobrama kuschakewitschi* corresponds exactly with that observed in the Chu, namely the largest numbers are to be found in the mouth of the back-

Table VII. *Distribution of native fishes in the Amu-Darja delta.*

Station	Abramis brama %	Cyprinus carpio %	pH	Trans- parency cm.	Minimum bottom productivity per sm. in mg.
Western Kara-Teren	36·3	13·6	7·5	254	140
Chilim-Kul	7·4	22·2	7·5	6	40
Eastern Kara-Teren	65·45	3·63	7·4	299	660

water, and toward the head they decrease. We had no opportunity of observing the shifting of the curves at night, as in the backwaters of the Chu; it may be that this does not occur at all in the backwaters of the Amu which we have explored. The occurrence of carp at the head of the backwaters may be best
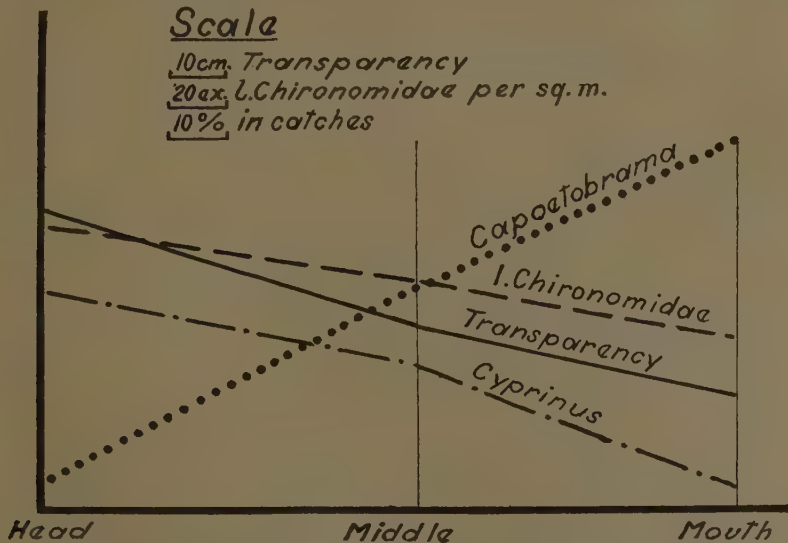
Fig. 6. Distribution curves of the backwaters: of transparency, of Chironomidae larvae per sq. m., and percentages in catches of *Cyprinus carpio* and *Capoetobrama kuschakewitschi*.

explained by the presence of abundant food, and not by the stagnancy of the water.

In conclusion we may say that the rate of flow in Central Asiatic rivers, especially in those running from the Tian-Shan, exercises a very strong influence on the distribution of fish; as Hesse (**9**) has pointed out, a change of

Table VIII. *Distribution of* Capoetobrama kuschakewitschi
and of carp in the backwaters of the Amu-Darja.

Station	Number of chironomids per sq. m.	Weight of chironomids per sq. m. mg.	Transparency cm.	*Capoeto-brama kuschakewit-schi* %	Carp %
Head	100	100	52	4·2	37·5
Centre	80	80	32	38·8	25·0
Mouth	60	40	20	65·0	3·8

the rate even on a very small portion immediately affects the composition of the fish communities.

A fish community in any given section of a river will contain the highest percentage of that species whose characteristics are best adapted to the conditions prevailing in that place. Thus, for overcoming the resistance of the current, the best adapted shape of the body of a fish is the torpedo streamline. Therefore we may expect that in streams with a swift current fishes with such a shape will predominate. The fishes with compressed sides will be numerically less important. For instance, the higher the body of a fish, the more difficult is it for it to resist a high rate of flow; even if such a species is able to swim against the current it will be at a disadvantage as compared with a species having a rounder shaped body. We may assume that the mean characteristics of a given community must correspond to a high degree with prevailing conditions; therefore, if we determine the typical shape of the body of a representative of a fish community in a given region, this shape must be considered the best reflection of the influence of local factors. In order to check the statement that in the community the leading characteristics must be at an optimum relation to the surrounding conditions, we compare the mean characters of fish communities in the river Chu, selecting for that purpose four related characteristics: viz. the height of the body (maximum) in percentages of the length of the body without the tail fin; the maximum width in percentages of the maximum height of the body; and the scapulary part or "cleithrum," in percentages of coracoid part. We then calculate the mean value of each character for samples of all twenty-five stations (separately for each station). For instance, the mean height of a species is multiplied by the percentage of this species in the sample; it is added up with the characters of other species and divided by the number of the specimens; the result is the average character of the sample. But in order to secure more accurate data it is necessary to deduct from the samples, when determining the mean characters, the predatory fish, because their structure (at least for Central Asia) has always a more or less torpedo-like shape adapted to the pursuit of their prey, whether a limnadophile or a roophile. For our analysis we selected the river Chu as the most thoroughly investigated by us, and in fact the data obtained confirmed our hypothesis. All the characters of the community undergo a regular alteration and constantly tend to attain the most perfect adaptation

to the local conditions. When any further alteration of character is un-
necessary, it becomes, so to speak, stabilised. Although individual members
of the community may possess such a character in a more developed degree,
if its further development is unnecessary the mean remains stationary. For
instance, the index of the cleithrum in the lower part of the Chu is 100–103,
and it has been stabilised at that figure, in spite of the fact that in individual
members of the community it is sometimes greater.

In this way the form of the body of the fish undergoes definite changes from
the upper to the lower part of the river. However, the ratio of resistance for
fish with a high body and for those which are torpedo-shaped does not greatly
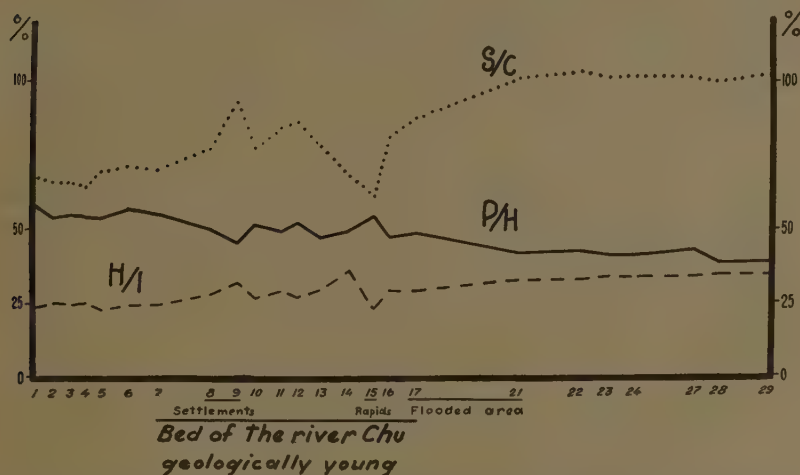
Fig. 7. Variation curves of the mean characters in fish communities along the course of the river
Chu. The upper part of cleithrum in percentages of the lower (s/c). Maximum width of body
in percentages of maximum height (p/h). Maximum height in percentages of length (not
including caudal fin) (h/l). Bed of the river Chu geologically young. Swift current. Settle-
ment.

differ. The principal difference is in the ratio of fullness, that is to say that for
the same surface the torpedo-shaped fishes possess a greater volume and con-
sequently have relatively greater strength to permit them to swim against
the current. But in the lower course, where this is not necessary, fishes with
a high body predominate; they are more enrigaline and better able to support
a more mineralised water.

The chart (Fig. 7) shows great variation in the curves of characters for the
middle course of the river from Station 8 to Station 16. In order to understand
this, we must take into consideration the history and the morphology of the
region. We find that the bed of the Chu "from the village Novotroitskoye to the
flooded areas below the village of Guliaevka flows through sands and ancient

quaternary sediments along a newly formed channel, sometimes very narrow, and therefore often causing a swift current and sand banks" (D. I. Jakovlev, (10)). This diversity in the individual stations and the changes in the channel, which sometimes flows rapidly between high banks and sometimes splits into arms and backwaters and forms pools of stagnant water, causes a great variation in the composition of the communities and naturally in the characters also. Hence I conclude that the more recent the channel geologically (and consequently, the greater the difference between stations), the greater the variety in the composition of the fish communities and the more variable the mean characters of the communities which exist at stations which, though near together, are of a different character.

In conclusion I must express once more my regret that the lack of adequate instruments prevented a more detailed investigation. I hope that the results accomplished may prove to be of some interest.

Summary.

A survey of the fish species of three Central Asiatic rivers showed that there are well-marked communities of species associated with different rates of flow of the rivers. Figures are given which suggest an adaptive correlation of shapes of the fishes with these physical conditions.

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A SURVEY OF NOCTURNAL VERTEBRATES IN THE KARTABO REGION OF BRITISH GUIANA

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THE purpose of this study was to survey the nocturnal activities of a large number of animals, preliminary to a general investigation of the nature of the nocturnal habit. Observations made on invertebrates will be reported separately. This problem would ultimately include a consideration of special adaptations for life in the darkness, and an analysis of the usefulness at night of the several senses, but these discussions are reserved for a later report.

Field observations were made in June, July and early August of 1924. Twenty-one night trips were made for the collection of data and specimens, as follows: fourteen near Kartabo Point, at the junction of the Cuyuni and Mazaruni rivers, 45 miles from the coast; one in the vicinity of Upper Camaria, 7 miles above Kartabo on the Cuyuni river; one on an island at Matope, 10 miles farther up the same stream; two from a base 4 miles south-west of Kartabo in the wedge-shaped tract between the Cuyuni and Mazaruni rivers; and three from Hills Estate, on the Mazaruni river near its junction with the Essequibo. Other trips at dusk and dawn (**8**), overlapping the hours of darkness, bring the total number of periods devoted to observation to thirty-two. Many records made at other times have been useful.

All of the places named above are in the low-tide-water area, with the exception of Matope, in the hills, and Upper Camaria, in rolling country at the head of a 4-mile rapid in the Cuyuni river. All of the localities are in the rain-forest area, but represent variously the conditions of deep jungle, open clearing, tide-water shore, and islands in inland rapids.

Meteorological data were recorded for each trip. Temperature can probably be disregarded as a possible factor affecting activity of vertebrates, since the gross variation during any one night, or even from one night to another, was never more than 6° F. In these months humidity also is remarkably constant, at about 85 per cent. Allee's (**1**) observations at Barro Colorado island also showed only small variations in barometric pressure, air temperature, air movement, and other environmental factors on the jungle floor. At Kartabo the chief variables were light (including moonlight), fog (affecting available light), wind, rain and tide (the last three named providing mechanical disturbance). The absence of light looms as the most characteristic factor of the nocturnal environment in the rain forest.

Records were made on form sheets of checkerboard style, with the names of animal forms in the left column, and with time intervals across the top of

the sheet. Only one check was made in a square, recording the activity of a particular animal at a certain hour. The relative frequency was thus not recorded, except that if the number of individuals was strikingly high or low at any time, the fact was noted, along with a statement of the conditions under which the species was active.

Observations were made both by silent and by active hunting methods. Sometimes the observer remained quiet in one spot for several hours, using artificial light only at intervals to identify animals heard. At other times a close-range search of bushes and ground was made with the flashlight for the detection of small forms. Another profitable method was the systematic sweeping of the jungle foliage and forest floor at long range with the flashlight held above the head, to get reflection from eyes. Regular visits were also made to marked stations. These included points on the beach and other open sandy places, straight-sided pits dug along the trails, tree-trunks and fallen logs in the deep jungle. Log landing-places extending into the rivers were very profitable stations for recording the activity of animals with loud calls. These sounds echoed along the rivers for great distances. In all cases of animals having easily recognised calls, these were accepted as evidences of activity, whether the individuals were seen or not.

This survey records the nocturnal activity of representatives of thirty-one families of vertebrates, not including any of the fishes. Amphibians and lizards are listed as in the writer's field keys (7). Birds are listed generally as in the A.O.U. check-list (2) and families of mammals are arranged as by Miller (9).

Class AMPHIBIA.

Order ANURA.

Family *Bufonidae.*

Toads, chiefly *Bufo marinis*, also *B. typhonius* and *B. guttatus*, were heard and seen all through the night, being most active for a few hours following dusk. Their eyes glowed when found with the flashlight. Captive specimens, sluggish during the day, began vigorous jumping after dark. Young toads are frequently diurnal, while old individuals tend to be crepuscular or nocturnal, but species doubtless differ among themselves in these respects.

Family *Hylidae.*

Tree-frogs of many species were heard from sunset to sunrise, being most vocal for a few hours following dusk. They are active to some extent by day, snapping up passing insects and calling occasionally, of course chiefly during the mating season. *Hyla rubra*, the most frequently observed species, enters dwellings at night and is apparently attracted to lights, including flashlights. *H. maxima*, also frequently seen, has an astonishingly loud call. *H. boans* and *Phyllomedusa bicolor* are common forms. *Hyla granosa* and *H. marmorata* were also taken at night.

Family *Ranidae.*

Many individual *Rana palmipes* were seen and heard all through the night, being most active before midnight.

Class REPTILIA.

Order CROCODILIA.

Family *Crocodilidae.*

A captive caiman was observed to be active all through the night, whether the moon was up or not.

Order LACERTILIA.

Family *Gekkonidae.*

The geckos were active in the bungalow all through the night. In the jungle they inhabit low stumps and logs. Occasionally they are active by day. *Thecadactylus rapicaudus* is the common nocturnal species.

Order OPHIDIA.

Family *Boidae.*

Captive boas, including the green tree boa, *Corallus caninus*, and the anaconda, *Eunectes murinus*, were observed to be very alert at dawn and dusk and just following dusk. Two anacondas were caught at nightfall at Matope, where they were hunting beside a stream.

Family *Viperidae.*

Beebe (4) notes the activity of the bushmaster, *Lachesis mutus*, at night.

Class AVES.

Order TINAMIFORMES.

Family *Tinamidae.*

The various tinamous were distinguished by their loud calls, which are made by individuals of both sexes, but chiefly the female. On an early morning trip, three tinamous were flushed just after daybreak, at intervals along a trail.

Pileated tinamou, *Crypturus soui.* These birds were heard chiefly for an hour before and after sunset and at dawn, but also occasionally through the night, especially in the few hours following midnight, and not always in the moonlight.

Variegated tinamou, *Crypturus variegatus.* This bird was heard just before daybreak.

Guiana great tinamou, *Tinamus major.* The calls of this bird were most frequently heard for half an hour after sunset, and for three-quarters of an hour before and after sunrise. Beebe (3) noted that on moonlit nights it called throughout the night.

Order CHARADRIIFORMES.

Family *Laridae*.

Terns had a nightly roosting place on a decaying "beacon" of timbers marking a shoal in the river, a mile downstream. The cries of these birds were heard at dusk and dawn, and at every hour of the night, as they were disturbed by wind, rain, or rising tide. Probably all were of the common genus *Phaetusa*.

Order STRIGIFORMES.

Family *Strigidae*.

The "spectacled owl," *Pulsatrix perspicillata*, was rarely heard. On one occasion an individual visited the clearing just before midnight. This bird spends its days in the branches of low trees. It flies noiselessly. Its call resembles a mammalian grunt. The eyes glow at night when illuminated.

Order CAPRIMULGIFORMES.

Family *Caprimulgidae*.

White-collared nighthawk, *Nyctidromus albicollis*. The querulous "Who-are-you" of this bird was a common and always startling call, heard most frequently just after dusk, in the early morning hours, and for a couple of hours following daybreak. "Who-are-yous" usually are seen and heard singly. Beebe (4) on one occasion found at least forty engaged in a sort of dance by moonlight on a sandy area. By day they roost on the ground, or on logs or low branches, in the jungle. At night they come to clearings and trailsides. Their eyes return a dull red glow when flashed with the electric torch.

Giant goatsucker, *Nyctibius griseus*. A "Poor-me-one," as this bird is known from its sighing call, was often heard across the Cuyuni river. Its call was most frequent from just before daybreak until nearly sunrise, but it was also heard between eight and nine in the evening. It spends its day in the thicker branches of low trees. Its eyes return light from the torch.

Class MAMMALIA.

Order MARSUPIALIA.

Family *Didelphidae*.

All of the opossums are nocturnal. The small species in the laboratory was chiefly active from 9 to 11 p.m. Opossum eyes return light from the flash.

Order CHIROPTERA.

The bats were active in flight from a half hour after sunset to within 15 minutes of sunrise, but were less numerous in the hours before dawn. By day they roost in hollow trees.

Family *Phyllostomidae*.

After dark, at Hills Estate, a fruit-bat with a wingspread of 23 inches was caught.

Family *Desmodontidae*.

Vampire bats were known to be at Kartabo (5), but were not definitely observed during our stay. On one occasion a bat, possibly a vampire, hovered for an instant about the writer's hand.

Other bats, chiefly of the families Vespertilionidae and Molossidae, were present in large numbers.

Family *Procyonidae*.   Order CARNIVORA.

Potos flavus, the kinkajou or "night monkey," active at night on branches of intermediate height, has eyes that return light from the electric flash.

Procyon, the crab-eating raccoon, is known to be active at night along the river banks.

Family *Felidae*.

The cats are active both by day and by night. They rest in trees and on logs. The genus *Felis* is represented locally by the jaguar, puma, ocelot, jaguarondi, and margay cat. The eyes of all these cats glow red when found with the searchlight. An ocelot or other cat of similar size was observed by us at intervals for an hour and a half following one o'clock at Upper Camaria. A jaguarondi was seen running rapidly through low brush at daybreak. Small cats staged duets at the edge of the compound about midnight and at three o'clock in the morning on two occasions.

Family *Cebidae*.   Order PRIMATES.

The red-howler monkeys, *Alouatta seniculus*, were heard at various hours from midnight on until half an hour after sunrise. They were most vocal from daybreak to sunrise.

Order RODENTIA.

Families *Muridae* and *Cricetidae*.

All of the rats are of course active at night. Those seen in the light of the flash could not be specifically identified.

Family *Erethizontidae*.

The tree porcupine, *Coendou*, is commonly nocturnal.

Family *Dasyproctidae*.

The agouti, *Dasyprocta croconota*, is quite common. One was disturbed on a jungle trip at 3 a.m. These swift rodents were doubtless among various unidentified animals which rushed away from the trail-side at night, before they could be found with the flashlight.

Family *Cuniculidae*.

The labba, *Cuniculus paca*, has habits similar to those of the agouti, is a larger animal, but is not so common.

Family *Hydrochoeridae.*

The capybara, *Hydrochoerus*, is described by both Beebe (**5**) and Roosevelt (**10**) as being nocturnal, feeding on swamp plants along the river shore. It is a guinea-pig, sometimes several feet in length.

Order ARTIODACTYLA.

Family *Tayassuidae.*

Peccaries were reported as active at daybreak, and probably had been abroad earlier.

Family *Cervidae.*

The genus *Mazama* is represented by two brockets, a larger and a smaller one, red and brown respectively. These are solitary jungle animals, active at night.

Order PERISSODACTYLA.

Family *Tapiridae.*

The bush cow or tapir, *Tapirus*, mentioned by Beebe as rare in the deeper Kartabo swamps, is reported by Roosevelt (**10**) as living "in dense cover, usually lying down in the daytime and at night coming out to feed, and going to the river or to some lagoon to bathe and swim."

Order XENARTHRA.

Family *Bradypodidae.*

The three-toed sloth, *Bradypus cuculliger cuculliger*, is arboreal and nocturnal, hanging by day in the Cecropia trees. Only captive ones were observed.

Family *Myrmecophagidae.*

Cyclopes, the arboreal silky anteater, is recorded by Beebe (**5**) as being nocturnal.

Family *Dasypodidae.*

The armadillos are solitary nocturnal animals. The rare giant armadillo, *Cabassous unicinctus*, captured by a half-breed, was active from sunset to daybreak. Other local armadillos, *Dasypus* and *Tatu*, may be found in the jungle at night.

SUMMARY.

Species representing thirty-one families of vertebrates other than fishes were found to be active at night in a portion of the rain-forest area of British Guiana centring about Kartabo. Fish were not studied. Observations made on the nocturnal activity of invertebrates will be reported separately. A statement of methods used in making the survey is included in the introduction. Comments on the various vertebrates observed make up the body of the paper.

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NOTES

ON A METHOD OF MARKING TSETSE FLIES.　　J.N.R

SEVERAL enquiries having been addressed to the writer on the details of a system of marking tsetse flies in the field alluded to in a previous paper (*Bull. Ent. Res.* 21, 495, 1930), it is thought that a short account of the method should be given.

Scott (*S. African J. of Science*, 28, 372–5, 1931) summarises the literature of the subject and notes that the oil paints used in this work were not injurious to the flies. He also describes a system of differential marking used by him and his co-workers, ingeniously providing for recognition of nine marking sites, three times of day, five conditions of hunger, and every day for nearly a year.

This system has obvious advantages, but is not suitable for all classes of work. The system evolved by the writer in 1929 gives a much smaller number of combinations (on initial marking) but has certain special advantages, not the least of which is that re-marking on recapture is provided for.

Flies are marked with oil paints on the back of the thorax. From two to five spots are applied on the initial marking. The paint is applied with a grass stem which should be dry and as thin as possible. The index finger of the left hand is placed under the fly's abdomen, and the tips of the wings are held down with the thumb. The paint is applied with the grass stem held in the right hand and placed horizontally across the thorax and slightly rotated. Only two colours are used on any one day, alternate ends of the grass stem being dipped into the two paints as required. This method allows of rapid marking with a minimum of apparatus to be carried about in the field, but a more important advantage is that the men catching the flies are able to see at once whether or not a fly has been marked on that day, by noticing simply what pair of colours it carries on its back. This assures that flies marked on previous days shall not escape recapture and re-marking, and that flies marked on the same day shall not be recaptured unnecessarily and the wet paint smudged.

The pair of colours used indicates the date of marking of the recaptured fly; their disposition indicates the place of release together with the hunger condition when released or any other particulars arranged for. As two, three, or four dots can be applied in the original marking it is evident that a considerable number of two-colour combinations can be used.

Colours which have given satisfactory results, as being easily distinguished in the field, are dark blue, light blue, dark green, light green, brown, vermilion, pink, orange, ochre, yellow, white, purple, and grey. These colours provide combinations for 78 days.

On recapture flies are marked with the two colours of the day of recapture. The recapture marks are placed on the periphery of the thorax, and do not

interfere with the original marking, which is now dry. Thus a fly marked origin-ally with two light blues on the left and one yellow on the right might indicate that it had been marked originally as hungry in locality A on the light blue-yellow date. On recapture on, say, the yellow-white day, it might be re-marked yellow on the right forecorner of the thorax and white on the left side. This mark would be recorded as 1.45 (or 2.45), the thorax being considered as the face of a clock, as is a target in shooting. If a second fly with the same original mark were recaptured on the same day, it would receive a different re-mark. Thus it might be marked yellow on the right side and white on the left hind corner of the thorax, the re-mark being written as 3.35 or 3.40. The re-mark is chosen arbitrarily except in so far as identical re-marks must not be given on any one day to individual flies having identical original markings.

As no two flies originally marked alike are given the same re-mark on any day, and the re-mark colours are changed daily with the colours for original marking, a fly once re-marked has no duplicate throughout the experiment, and will need no further re-mark if captured again.

Recaptured flies are best recorded on sheets ruled with columns for the date, hunger condition, and original mark given to the fly at the time of its first being captured, and the same particulars for the time of recapture. Ad-ditional columns are provided for cross-references to other sheets in the experiment, the sex of the fly, and the number of days elapsing between marking and recapture. The cross-references will refer to flies several times captured. Usually it is best to record on different sheets flies moving to or from different localities. Thus all flies moving from A to B will be recorded on one sheet or set of sheets, while other sheets will record flies moving from B to A or from A to C. The histories of flies several times captured can be extracted from these sheets and recorded separately if desired.   C. H. N. JACKSON.

IMMIGRATION OF ROOKS FROM THE CONTINENT TO ENGLAND.

IN this *Journal* (2, 34) I stated that the only ringed Rook from abroad re-covered in the British Isles was one obtained in the East Riding of Yorkshire in December, 1930, which had been ringed at a lightship off Borkum in October, 1927. Recently five additional recoveries have been reported, viz.:

Place and date of ringing	Place and date of recovery
Hanover, Germany, May, 1931 (nestling)	Suffolk, November, 1931
,, ,, ,, ,,	Essex, January, 1932
,, ,, ,, ,,	Norfolk, March, 1932
Raseiniai, Lithuania ,, ,,	,, October, 1931
Near Leningrad, Russia, Spring, 1932	,, February, 1933

(*British Birds*, 25, 357 and 26, 352.)

These records give strong support to the conclusion reached from the study of the numbers of rooks in summer and winter in the Upper Thames district and near Cambridge that the majority of the foreign rooks which winter in England remain in the eastern counties.   W. B. ALEXANDER.

NOTICES OF PUBLICATIONS ON ANIMAL ECOLOGY

1. GENERAL PAPERS ON PARTICULAR GROUPS OF ANIMALS.

51. Bristowe, W. S. (1933). "The British species of *Atypus*." Ann. and Mag. Nat. Hist. 11, 289–302.

There is probably only one species in the British Isles, where it occurs in southern England, Wales, and Ireland. The habits are described in relation to its subterranean nest, soils, etc.

52. Nicholson, C. (1933). "*Spilocryptus saturniae* Boie (Ichneumonidae) in Britain." Entomologist, 66, 109–11.

A parasite of *Eudia (Saturnia) pavonia* L. Contains a key for identification of five species of *Spilocryptus*, occurring in England.

53. Hobby, B. M. (1932). "A key to the British species of Asilidae (Diptera)." Trans. Ent. Soc. S. Engl. 8, 45–9.

54. Turk, F. A. (1933). "A preliminary list of British Collembola." Trans. Ent. Soc. S. Engl. 8, 92–7.

124 species occur in Britain.

55. Audcent, H. (1932). "British Tipulinae (Diptera, Tipulidae)." Trans. Ent. Soc. S. Engl. 8, 1–34.

Keys to the 74 British species.

56. Moore, H. B. (1933). "The faecal pellets of the Anomura." Proc. Royal Physical Soc. Edinburgh, 52, 296–308.

A study of British crabs, to assist identification of faecal pellets in fossil deposits; there are well-marked differences between different crabs.

57. Leigh–Sharpe, W. H. (1933). "The Hirudinea of Plymouth. Part I." Parasitology, 25, 255–62.

Marine leeches.

58. Ullyott, P. (1932). "Notes on *Planaria vitta* Dugès." Q. J. Micr. Sci. 75, 482–94.

A white planarian found in the Lake District and Wales is described. It had previously been confused with another continental species.

2. ECOLOGICAL SURVEYS AND HABITAT NOTES.

(a) MARINE.

See also **111, 125, 126, 139.**

59. Gray, R. W. (1932). "Breeding places of the saddle or harp seal." Naturalist, 183–6.

This species is pelagic in the Arctic seas, feeding and breeding on the edge of the polar pack. Its food is Crustacea.

60. Gillespie, A. S. (1932). "Notes on the sandy shore fauna of Colwyn Bay." North Western Nat. 7, 23–6.

General notes on the conspicuous species and their habitats.

61. Gillespie, A. S. (1933). "The distribution of some common rocky shore animals: with special reference to the west coast of Anglesey." North Western Nat. 8, 114–20.

Gives the general zonation of species relative to algal zones, substratum, and high and low water marks (no details of tidal rhythms given).

62. Renouf, L. P. W. (1933). "Some air-breathing arthropods of the littoral region of the coast of County Cork, I.F.S." Ann. and Mag. Nat. Hist. 10, 262–7.

63. Gardiner, A. C. (1933). "Vertical distribution in *Calanus finmarchicus*." J. Marine Biol. Ass. 18, 575–610.

Hardy's "plankton indicator" was used in a study of this copepod in the spring fishery area off Shields.

<center>(b) FRESHWATER.</center>

<center>See also **58, 75.**</center>

64. Oldham, C. (1933). "The palmated newt, *Molge palmata* (Schneider) in Wales." North Western Nat. 8, 105–10.

This paper covers much more than its title, including as it does references to distribution throughout the British archipelago, also discussion of other newt species. All three species occur together at times, but the smooth newt inhabits a wider range of ecological conditions.

65. Balfour-Browne, F. (1933). "The aquatic Coleoptera of the Channel Islands." Ent. Mo. Mag. 69, 67–77.

66. Smith, S. H. (1932). "Distribution of the freshwater crayfish in Yorkshire, 1932." Naturalist, 372–3.

67. Oldham, C. (1932). "Notes on some Scottish and Shetland *Pisidia*." J. Conchology, 19, 271–8.

Contains much ecological information about the occurrence of these freshwater bivalves, also other aquatic molluscs, which are eaten in large numbers by trout.

68. Ellis, A. E. (1932). "Further localities for *Planorbis vorticulus* Troschel." J. Conchology, 19, 258–9.

Notes on the restricted distribution of this water snail, together with lists of its associates (molluscs, some other animals, and plants).

<center>(c) LAND.</center>

<center>See also **107, 122.**</center>

69. Boycott, A. E. (1933). "Local lists of animals." Nature, 131, 94–5.

A protest against criticism of local lists, which are of importance in compiling accurate distribution maps for British animals, and also in comparing distribution now and in the past. It is pointed out that in view of this usefulness, the making of local lists forms a healthy and desirable focussing-point for the work of local naturalists.

70. Austin, M. D. (1933). "The insect and allied fauna of cultivated mushrooms." Ent. Mo. Mag. 69, 16–19 and 132–4.

71. Richards, O. W. (1932). "Insects bred from a rotten oak-branch in Windsor Park." Proc. Ent. Soc. London, 7, 41.

Seven species of Diptera.

72. Donisthorpe, H. (1932). "The Coleopterous fauna of a willow swamp in Windsor Forest." Ent. Rec. 44, 4–6. See also Proc. Ent. Soc. London, 7, 29–30 and 40.

About 170 species of Coleoptera have been captured in this willow swamp. Notes on habitat are given.

73. Richards, O. W. (1932). "Insects bred from fungus in Windsor Park." Proc. Ent. Soc. London, 7, 42–3.

The following were bred from a dead and dry fungus (*Polyporus hispidus*) taken from an ash: *Tinea cloacella* (Lep.); *Orchesia micans*, *Cryptophagus fowleri* (Col.); *Cryptoserphus parvulus*, *Diaparsus gilvipes*, *Meteorus obfuscatus* (Hym.). The *Meteorus* is a frequent parasite of *Orchesia*; on the continent *Diaparsus* has been bred from a close ally of *Orchesia*. *Cryptoserphus* is a parasite of Mycetophilid flies; possibly at the time when the fungus was collected the hosts had already emerged. From a living fungus (*Fomes fomentarius*), obtained from a beech, a Tineid moth (*Scardia boleti*) was bred. **K. G. Blair** adds a list of insects bred from a fungus taken from an elm.

74. Laidlaw, W. B. R. (1933). "Entomological notes from Ullapool (Ross-shire)." Scottish Nat. 55–9.

Casual records of a number of different insects, with some data about habitats, especially those of *Bombus* species.

75. Walker, J. J. (1932). "An annotated list of the Coleoptera of the Isle of Sheppey." Trans. Ent. Soc. S. Engl. 7, 81–140.

Of the 3587 species found in the British Isles 1211 are recorded from Sheppey. For these, localities, habitats and some indication of abundance are given. The pasture lands are not very productive in beetles and wood-feeders are poorly represented. No large sheets of standing water and only two insignificant running streams are to be found in the island, but the innumerable ditches, more or less fresh inland and brackish near the shore, yield a number of interesting beetles. The mixed herbage on the cliff-edges and the salt marshes also produce many species.

76. Killington, F. J. (1932). "A contribution towards a biological survey of the Megaloptera and Neuroptera of Hampshire and the Isle of Wight." Trans. Ent. Soc. S. Engl. 7, 56–67.

Of the 59 British species 46 occur in Hampshire; a detailed account of the distribution of these within the county is given. An ecological grouping of the British species based where possible upon larval habitats, a table of the months in which the imagines have been taken and a list of Hymenopterous parasites are given.

77. Killington, F. J. (1932). "Notes on the life-history of *Hemerobius pini* Steph. (Neuroptera)." Trans. Ent. Soc. S. Engl. 8, 41–4.

This species is exclusively attached to conifers and is apparently at least double brooded. Twenty-two specimens were taken in the webs of the spider *Linyphia peltata* and one as prey of a Cordylurid fly.

78. Butterfield, R. and **Fordham, W. J. (1932).** "Aculeate Hymenoptera of Yorkshire." Naturalist, 233–6, 256–9, 279–82, 309–11; and 1933, 69–70.

Contains a number of habitat notes. (See also **Fordham,** Scottish Nat. 1933, 119.)

79. Richards, O. W. (1932). "Observations on the genus *Bethylus* Latr. (=*Perisemus* Forest) (Hymenoptera, Bethylidae)." Trans. Ent. Soc. S. Engl. 8, 35–40.

Gives a summary of the literature referring to the primitive wasps *Bethylus cephalotes* and *B. fuscicornis*. The former preys upon Noctuid larvae and is recorded amongst reeds, roots of grass, in hedges, on oak trees and in ants' nests, although it is possible that the ants' nest specimens may be a distinct species. Descriptions of the early stages of *B. cephalotes* are given. *B. fuscicornis* attacks Tineid and Tortricid larvae and nests in stems.

80. Benson, R. B. (1933). "Arctic Ichneumonidae in the Perthshire Highlands, including several species new to Britain." Ent. Mo. Mag. 69, 79–81.

81. Edwards, F. W. (1933). "Some Perthshire Diptera." Scottish Nat. 87–92 and 113–17.

Includes some interesting geographical records from Perthshire mountains, e.g. the Mycetophilid fly *Macrocera zetterstedtii* previously known only from Scandinavia, and the Chironomid fly *Metriocnemus ursinus*, previously known only from Spitsbergen and Bear Island.

82. Basden, E. B. (1933). "On some species of the genus *Sciara* (Dipt., Mycetophilidae) from the nests of birds and mammals." Ent. Mo. Mag. 69, 44.

A list of seven species and their habitats.

83. Imperial Bureau of Agricultural Parasitology (1931). "The root-infesting eelworms of the genus *Heterodera*: a bibliography and host list." 1–99.

Includes also a summary of their general ecology.

3. ANIMAL BEHAVIOUR AND THE ACTION OF ENVIRONMENTAL FACTORS.

See also **51, 113, 115–17, 121.**

84. Hardy, E. (1933). "On the habits of the red squirrel as observed at Liverpool." Naturalist, 53–6.

Useful observations over a period of ten years. They cover territory habits in the breeding season, winter movements, food, drinking habits, breeding, disease, courtship, and relation to the grey squirrel (not found at Liverpool, but studied in Midland counties). Fighting occurs between the two species, but the grey was not observed to drive away the red. Red squirrels are increasing after a period of disease some years ago.

85. Walsh, G. B. (1933). "Studies in the British necrophagous Coleoptera. II. The attractive powers of various natural baits." Ent. Mo. Mag. 69, 28–32.

Experiments showed that fairly pure fat has relatively small attraction; those baits which most quickly decompose are most attractive. It is suggested that a nitrogen compound, possibly of an amino nature, in decomposition products acts as the attractant.

86. Adkin, R. (1933). "The light-trap as an adjunct to the exploration of a fauna." Entomologist, 66, 123–9.

Includes a useful list of Lepidoptera attracted to light. Further reference in **C. de Worms**, Entomologist, 66, 140–1.

87. Balfour-Browne, F. (1933). "The life-history of the 'small eggar moth' *Eriogaster lanestris* L." Proc. Zool. Soc. London, 161–80.

An elaborate study of this social caterpillar and its web-building habits. Migration was studied, and caterpillars were found to maintain their original direction when progress was interrupted and positions changed.

88. Orton, J. H. (1933). "Some limiting factors in the environment of the common limpet, P. vulgata." Nature, 131, 693–4.

Dead and dying limpets were found at the edge of rock pools near Padstow, at a time when calm and rather warm weather and low summer neap tides had caused unusually long exposure of the molluscs.

89. Cooper, L. H. N. (1933). "Chemical constituents of biological importance in the English Channel, November 1930 to January 1932." J. Marine Biol. Ass. 18, 677–728 and 729–53.

From extensive chemical data the phytoplankton crop was calculated to be in the neighbourhood of 1400 metric tons (wet) per square km. of surface, and the amount harvested by fish was estimated to be 0·06 per cent. of this.

90. Atkins, W. R. G. (1933). "The photoelectric measurement of the penetration of light of various wave-lengths into the sea and the physiological bearing of the results." Phil. Trans. Royal Soc. London, B, 222, 129–64.

91. Pearsall, W. H. and Ullyott, P. (1933). "Measurement of light for biological purposes." Nature, 131, 694.

Describes an improved type of apparatus for measurement of light under water, consisting of a Bernheim photo-voltaic cell which is read by a galvanometer.

92. Reid, D. M. (1932). "Salinity interchange between salt water and sand and overflowing fresh water at low tide. 2." J. Marine Biol. Ass. 18, 299–306.

Further quantitative analysis (including the time element) of the salt-retaining power of the water in mud when fresher water is flowing over it during low tide periods.

93. Alexander, W. B., Southgate, B. A. and Bassindale, R. (1932). "The salinity of the water retained in the muddy foreshore of an estuary." J. Marine Biol. Ass. 18, 297–8.

As shown by Reid, the water in estuarine mud at low tide is very much more saline than that flowing over it. This affects the powers of penetration of marine animals into estuaries, the burrowing forms going in farther from the sea than the non-burrowing forms, as proved by analysis of quantitative census figures. This occurs both in the Tees and the Tay.

94. Baker, J. N. L. (1932). "The climate of England in the seventeenth century." J. Royal Meteorol. Soc. 58, 421–39.

A review of diaries and other historical records throws doubt on the validity of deducing the climate of past centuries from casual records, and stresses the danger of basing theories on anything but regularly kept meteorological records.

95. Barnes, A. A. (1932). "Rainfall reviewed. A common long-average period for each country of the British Isles." Q. J. Royal Meteorol. Soc. 58, 126–49.

Gives curves of cumulative differences from the mean ("residual mass curves") of annual rainfall for England and Wales, Scotland, Ireland, and British Isles, for the years 1887–1930. There is a strongly marked cycle of about 37 years shown by this method of plotting the figures. This affects the averaging of rainfall data, the mean obtained in different series of years varying nearly 2 per cent. The cycle is similar to that of Brückner's cycle which is shown in historical data for European climate, and the author suggests that we are at or near a maximum which will be followed by twelve years (average) dryness. Doubt is thrown on this conclusion in the discussion of the paper by other meteorologists.

4. PARASITES OF ANIMALS.

96. Jones, A. P. (1933). " *Lipoptena cervi* L. in Notts: Additional Note." Ent. Mo. Mag. 69, 65.

Abundance of this Dipterous parasite of deer. See **24.**

97. Hayward, H. C. (1933). "The contrast between the Geometrid moths *Eupithecia albipunctata* Haw., and *E. trisignaria* Herr.-Sch., in the production of dark forms and the liability to the attacks of parasites, in the neighbourhood of Repton." Proc. Ent. Soc. London, 7, 73–5.

Near Repton *E. albipunctata* is much attacked by parasites while *E. trisignaria* is almost immune, although the larvae are of the same size and occur on the same plant at the same time. Twenty years ago *E. albipunctata* larvae outnumbered *E. trisignaria* larvae by more than ten to one. The latter is now the commoner of the two, and from several once well-tenanted localities *E. albipunctata* seems to have entirely disappeared.

98. Killington, F. J. (1933). "The parasites of Neuroptera with special reference to those attacking British species." Trans. Ent. Soc. S. Engl. 8, 84–91.

The majority of known parasites are Hymenoptera; other parasites include a bacterium, a protozoan, a mite and a Dipteron. No parasites of the egg are known from Britain but a number have been noted abroad. The active larval stage and prepupal stage are much attacked, but there is little evidence of attacks on pupae. A midge, *Forcipomyia eques*, has been found both in America and Europe attached to the wings of adult Chrysopidae.

99. Marriner, T. F. (1932). "A Coccinellidae parasite." Naturalist, 221–2.

A parasitic fly, *Phalacretophora fasciata*, was found to cause mortality among larvae of various species of ladybirds kept in captivity, and is apparently commoner in dry seasons.

100. Petch, T. (1932). "British entomogenous Fungi." Naturalist, 167–72.

The concluding section of a useful account of fungi that attack insects.

101. Leigh–Sharpe, W. H. (1933). "A list of British fishes with their characteristic parasitic Copepoda." Parasitology, 25, 109–12.

Freshwater and marine fishes.

102. Leigh–Sharpe, W. H. (1933). "A second list of parasitic Copepoda of Plymouth with a description of three new species." Parasitology, 25, 113–18.

5. FOOD-HABITS.

103. Fraser, A. H. H. and Robertson, D. (1933). "Nutritional condition of sheep and susceptibility to stomach worm." Nature, 131, 94.

Differential feeding experiments showed that the average infestation was significantly greater in poorly fed sheep.

104. Collenette, C. C. (1933). "Butterflies as prey of birds." Scottish Nat. 54.

An appeal both for original records of adult butterflies being attacked by birds, and for references to scattered published notes. These should be sent c/o Entomological Department, British Museum (Natural History), London, S.W. 7.

105. Poulton, E. B. (1933). "Wings of British, European and N. American butterflies bearing the marks of attack by enemies, chiefly birds." Proc. Ent. Soc. London, 7, 71–3.

The list includes representatives of the following genera: *Epinephile, Adelpha, Limenitis, Polygonia, Vanessa, Ganoris, Pieris, Anthocaris, Gonepteryx, Nemeobius* and *Parnassius.* See also *ibid.* 7, 10–11, and **J. F. Perkins**, *ibid.* 7, 11 for further evidence of attacks of birds upon butterflies.

106. Poulton, E. B. and others (1933). "Protective adaptations of animals— especially insects." Proc. Ent. Soc. London, 7, 79–105.

A discussion chiefly focussed on W. L. McAtee's contention that availability is the most important factor involved in the choice of food by birds, and "that the phenomena classed by theorists as protective adaptations have little or no effectiveness." This thesis receives little support from the numerous speakers, who criticise McAtee's statistical methods, draw attention to much previously published work and bring forward new evidence bearing on this question. **H. B. Coot** in a striking account of the food of Amphibia records that 148 toads had eaten 4103 ants but that only 7 ants were recovered from the 90 frogs examined.

107. Metcalfe, Margot E. (1933). "Some Cecidomyidae attacking the seed of *Dactylis glomerata* L. and *Lolium perenne* L." Ann. Appl. Biol. 20, 327–41.

Biologies of three species, two of which are described for the first time. From attempts to induce them to oviposit on other grasses, it appears that these gall midges are specific in their host plant.

108. Hobby, B. M. (1933). "The prey of British dragonflies." Trans. Ent. Soc. S. Engl. 8, 65–76.

Dragonflies are the chief predatory insect enemies of "aquatic" insects, and not only attack Ephemeroptera, Megaloptera, Plecoptera and Trichoptera but also their own order. Bees and wasps are possibly specially attacked by *Cordulegaster annulatus* and other Aeschnidae.

109. Hobby, B. M. (1932). "Observations on the habits and prey of the Fossorial wasp, *Mellinus arvensis* L." Trans. Ent. Soc. S. Engl. 7, 68–80.

Gives a list of 352 Dipterous prey, including 65 species—largely "Muscidae" (*sens. lat.*).

110. Hobby, B. M. (1932). "The prey of sawflies (Hym. Tenthredinidae)." Proc. Ent. Soc. London, 7, 14–15 and 35–6.

Many sawflies take no food as adults, others feed on pollen and nectar, while some, especially those of the genera *Tenthredella, Tenthredo, Macrophya, Tenthredopsis, Rhogogaster* and *Taxonus,* are predacious.

111. Dennell, R. (1933). "The habits and feeding mechanism of the Amphipod *Haustorius arenarius* Slabber." J. Linn. Soc. 38, 363–88.

This crustacean lives in wet sand, usually between tide-marks, all round the British coast. An area in Robin Hood's Bay showed sharp gradients in the wetness of sand, with which the abundance of *Haustorius* was correlated. It seeks the wetter sand from the water of which it obtains small organic particles for food by means of a special filtering apparatus on the appendages.

6. THE NUMBERS OF ANIMALS.

See also **63, 84, 88, 89, 99, 139.**

112. Fortune, R. (1932). "The grey squirrel in Wharfedale." Naturalist, 226–7.

In this area red squirrels had decreased greatly before the arrival of the grey. A grey squirrel was, however, seen to catch and kill a red one.

113. Boyd, A. W. (1932). "A great Cheshire starling roost in 1930." North Western Nat. 7, 10–18.

Full account of this roost, with map of territory served by it and notes on times of arrival and departure of birds. Also a list of parasites found on the starlings (bird-lice and feather-mites).

114. Cramp, S. (1933). "Starling roosts in North-West Cheshire." North Western Nat. 8, 111–14.

In 1930 most of Cheshire was served by one big roost. This paper describes changes during the following two years.

115. Graham, R. (1933). "Changes in the distribution of British geese: the Solway Firth (Cumbrian side)." Scottish Nat. 47–53.

Analysis of a number of records over the last 45 years shows that the bean goose has steadily decreased since about 1890, but that the grey lag and pinkfooted geese steadily increased, the latter reaching its greatest numbers about 1913, and the former being now the most abundant.

116. Coombes, R. A. H. (1933). "Changes in the distribution of British grey geese." Scottish Nat. 65–72.

Does not subscribe to the theory that the main cause of changes is to be sought in the food supply in Britain. The chief change noted is the increase of grey lag geese, colonising new areas in England, Scotland and Ireland, and the spreading of pinkfooted geese in England. These, the writer suggests, must be due to the onset of more favourable conditions in the northern arctic breeding grounds.

117. Beveridge, G. (1933). "On the changes in the distribution of wild ducks in North Uist (both of the surface feeding and non-surface feeding ducks)." Scottish Nat. 109–12.

Notes decrease of wigeon, mallard, teal, gadwall, and pochard in recent years. The decrease of wigeon is partly due to diminution and local disappearance of the eel-grass, *Zostera marina*, upon which they feed. Eider ducks have increased.

118. Tucker, B. W. (1933). "Report of the Oxford Ornithological Society on the birds of Oxfordshire, Berkshire, and Buckinghamshire, for 1932." Proc. and Rept. Ashmolean Nat. Hist. Soc. of Oxfordshire for 1932. Supplement.

This report includes several different studies and sets of records, mainly consisting of facts with few general conclusions. (*a*) The annual notes on occurrence, numbers, and movements of various species; (*b*) studies of the local distribution of the stonechat and whinchat, without definite accurate ecological descriptions of the habitats; (*c*) the breeding distribution of the redshank in the district, as a preliminary to more complete census work; (*d*) recovery of ringed birds, ringing of nestlings, and ringing of trapped birds in at least three trapping stations; (*e*) an expanded account of the great crested grebe census work (which had only been summarised for the district in Harrisson and Hollom's national census); (*f*) an account by **H. M. Wallis** and **J. D. Wood** of bird life at Reading Sewage Farm during the years 1922–32.

119. Booth, H. B. (1933). "The great crested grebe enquiry and census of 1931, in Yorkshire, and a few later notes." Naturalist, 87–92.

120. Holte MacPherson, A. (1933). "Gannets in Shetland." Scottish Nat. 118.

Notes on the history of certain colonies.

121. Hamilton, D. (1933). "Increase of the goldcrest in Midlothian." Scottish Nat. 45–6.

Gradual recovery towards abundance, after being decimated by the severe winter of 1916–17.

122. Bristowe, W. S. (1933). "Notes on the biology of spiders. 8. Rare spiders and the meaning of the word 'rare.'" Ann. and Mag. Nat. Hist. 11, 279–89.

Points out examples of species which are rare in the sense of having a very restricted or local distribution, but are abundant where they do occur, e.g. *Oonops domesticus* which creeps over the walls and ceilings of houses at night, also several spiders occurring in Wicken Fen.

123. Metcalfe, Margot E. (1933). "*Dasyneura leguminicola* (Lint.), the Clover Seed Midge." Ann. Appl. Biol. 20, 185–204.

Life history at Harpenden. English clover seed midge proved to be same species as that in U.S.A. and Canada. No immune varieties of clover were found, but the extent of attack was found to depend on the time of flowering of the clover and the emergence of adult midges.

124. Oldham, J. N. (1933). "Helminths in the biological control of insect pests." Imperial Bureau of Agricultural Parasitology, Notes and Memoranda, 9, 1–6.

Stresses the importance of parasitic worms in causing mortality among insects, e.g. a certain nematode was found parasitically castrating about forty per cent. of two species of elm bark beetles (*Scolytus*).

125. Elmhirst, R. (1932). "Studies in the Scottish marine fauna. The Crustacea of the sandy and muddy areas of the tidal zone." Proc. Royal Physical Soc. Edinburgh, 51, 169–75.

An independent study of the crustacean materials collected during A. C. Stephen's Clyde survey (which dealt with polychaete worms and molluscs). Most of the Crustacea were Amphipoda (Haustoridae being dominant in the sand and *Corophium* in the mud), and they showed strong zonation of occurrence and numbers. *Bathyporeia guilliamsoniana* was abundant in the *Tellina-Nephthys* (mollusc and polychaete) sandy areas, and *Corophium volutator* in mud. The data are recorded with Stephen's stations.

126. Pirrie, M. E., Bruce, J. R. and Moore, H. B. (1932). "A quantitative study of the fauna of the sandy beach at Port Erin." J. Marine Biol. Ass. 18, 279–96.

Exact chemical, physical, and biological (census) studies of five belt transects on the shore of Port Erin Bay, Isle of Man, are recorded. Seventeen species were found (mostly Crustacea and polychaete worms). No living molluscs occurred, in marked contrast to the results of surveys in the Clyde area. This is attributed mainly to greater exposure, other factors also being discussed.

7. MIGRATION AND DISPERSAL.

See also **63, 84, 87, 98, 118.**

127. Hewat Craw, J. (1933). "Exotic mammals on the Border." History of Berwickshire Nat. Club, 28, 108.

An American mink was caught in a rabbit trap on Pawston Hill in March 1930.

128. Perry, R. K. (1932). "Muskrat at Freshfield." North Western Nat. 7, 34.

Taken in May 1931.

129. Snowdon, F. (1933). "Waxwings in the Whitby district, 1932–33." Naturalist, 101–2.

130. Marples, G. (1932). "Homing tits." North Western Nat. 7, 26–7.

Blue tits (23 experiments), marsh tit (1 experiment), and great tits (2 experiments) taken in bird trap and liberated at distances of from half a mile to a mile mostly found their way back to the trap. There were 21 recoveries out of 26 experiments.

131. Stephen, A. C. (1933). "A rare shark (*Oxynotus paradoxus*) new to Scottish waters." Scottish Nat. 85–6.

Another example of recent occurrences of unusual foreign marine animals in British waters. Others mentioned are the long-finned tunny, the Saury pike (see notes by **J. Ritchie** and by **A. C. Stephen**, Scottish Nat. 1933, 39, and 95–6), certain squids, whales, and dolphins.

132. Clarke, W. J. (1933). "Saury pike (*Scombresox saurus*) at Scarborough." Naturalist, 100.

Unusual migration along the Yorkshire coast in winter 1932–33.

133. Fassnidge, W. (1933). "Immigration Records." Entomologist, 66, 17–20.

Notes on immigrant Lepidoptera. Further references in **F. W. Frohawk,** *ibid.* 27; **A. A. Dorrien Smith**. *ibid.* 6; **E. A. Cockayne,** *ibid.* 30; **C. Nicholson,** *ibid.* 67–8; **N. D. Riley,** *ibid.* 87; **R. Adkin,** *ibid.* 93–4; **W. Fassnidge,** *ibid.* 135; etc.

134. Dannreuther, T. (1932). "Records of immigrant Lepidoptera seen at Hastings (East Hill), with dates on which specimens were on the wing." Ent. Rec. 44, 156–7.

135. Williams, C. B. (1932). "Notes on some migratory butterflies." Proc. Ent. Soc. London, 7, 75.

A migratory flight of *Pieris rapae* was observed at Harpenden in August, 1932.

136. Main, H. (1932). "Recent insect immigrants." Proc. Ent. Soc. London, 7, 24.

A large cockroach, several beetles, a beetle larva, several spiders, millipedes, geckos and a skink were recently found as stowaways among imported goods.

137. Wakeley, S. (1933). "*Aphomia gularis* (Zeller) in Britain." Entomologist, 66, 99.

A species of Galleriadae from Eastern Asia that might become a serious pest at docks and in warehouses.

138. Russell, F. S. and **Hastings, A. B. (1933).** "On the occurrence of pelagic tunicates (Thaliacea) in the waters of the English Channel off Plymouth." J. Marine Biol. Ass. 18, 635–40.

Certain Atlantic species of *Doliolum* and *Salpa* were abundant in 1930–32. They are common inhabitants of the warmer seas of the world, and may be useful indicators of the influx of warmer currents.

139. Russell, F. S. (1933). "On the biology of *Sagitta*. 4. Observations on the natural history of *Sagitta elegans* Verrill and *Sagitta setosa* J. Müller in the Plymouth area." J. Marine Biol. Ass. 18, 559–71.

These *Sagittas* have well-marked seasonal fluctuations in the upper plankton, with great decrease in winter. The latter is due to their descent to lower layers and not to real decrease. Vertical movements are discussed on the basis of extensive plankton hauls throughout the year. *Sagitta* goes higher at night.

140. Schlesch, H. (1932). "*Petricola pholadiformis* Lam. in Europe." Naturalist, 213–4.

The limited spread of this introduced American mollusc appears to be related to the direction of currents distributing the young. It occurs also in Belgium and Denmark, but does not go north of the Humber on the British coast, nor south of Shellness, near Deal.

141. St John Burton, E. (1930). "The distribution of the slipper-limpet (*Crepidula fornicata* L.) in Britain." Proc. Bournemouth Nat. Sci. Soc. 22, 56–8.

Notes on the spread of this species, which now comes as far west as Swanage in Dorset.

Note. Attention is drawn to the publications of the *Entomological Society of the South of England*. The *Journal* (Vol. 1, Nos. 2 and 3, 1933, price 2*s*. 6*d*. each), which has not been abstracted here, contains a number of valuable short notes

on British insects, many of them ecological in content. Two of the longer papers deal with the preys of Asilid flies and of Dung flies.

The *Transactions of the Society* contain the first part of an important series of reports entitled "A bibliography of entomological notes and papers contained in the serial publications issued by local scientific societies in the British Isles," and edited by B. M. Hobby. The co-operation of various workers has been enlisted with the object of tabulating by titles (and in certain cases very brief abstracts) all papers and notes on British insects contained in these journals during past years. The present instalment covers the following periodicals: *J. Torquay Nat. Hist. Soc.* 1909–30; *J. of Proc. Winchester and Hants Sci. Lit. Soc.* 1870–9; *Papers and Proc. Hants Field Club and Arch. Soc.* 1885–1929; *Proc. Dorset Nat. Hist. and Antiqu. Field Club*, 1877–1928; *Proc. Isle of Wight Nat. Hist. Soc.* 1920–30; *Rept. Oxfordshire Nat. Hist. Soc. and Field Club and of Ashmolean Nat. Hist. Soc.* 1901–30; *Rept. and Trans. Devon Ass. Adv. Sci.* 1863–1931; *Trans. Hants. Ent. Soc.* 1924–28; *Trans. Penzance Nat. Hist. and Antiqu. Soc.* (discontinuously 1845–99, with varying title as *Trans.* or *Rept.*).

REVIEWS

THE AUGUST ISSUE OF THE *JOURNAL OF ECOLOGY* (VOL. XXI, NO. 2).

THIS number contains thirteen original contributions of very various nature. There are three general descriptions of vegetation, one relating to the Arctic and two to the Tropics. Mr Trapnell contributes a very thorough analysis, illustrated by excellent photographs, of the vegetation surrounding Godthaab Fjord in south-western Greenland; Messrs Davis and Richards the first part of their work on Moraballi Creek, British Guiana, one of the most complete studies of a small area of tropical rain-forest that has been undertaken; and Mr J. G. Myers interesting notes of a journey through the Venezuelan Llanos, whose vegetation is still very little known. He shows that they belong to Bews' types of *bunch-grass savanna* and *high-grass savanna*, and gives the names of the dominant grasses and of the savanna trees.

Mr R. E. Moreau, whose interest is primarily ornithological, writes on the Pleistocene changes of climate in East Africa, and shows that periods of desiccation, probably corresponding with northern "interglacials," have restricted the once continuous evergreen forest to small and mainly mountain areas. He thinks that comparatively small increase in rainfall or decrease in temperature would suffice to re-establish the forest over much wider areas.

Miss Conway continues the series of observations by members of the Cambridge Botany School, begun twenty years ago, on the changes in the topography and vegetation of the saltmarsh at Holme-next-the-Sea, Norfolk, and gives a large map identical in scale and design with the late Capt. Marsh's, published in 1913. Such continuous observations and records of topographic and successional change are extremely valuable. Dr Nellie Carter concludes her study of the alga flora of the Canvey and Ynyslas saltmarshes with a most useful and informative description of the algal communities.

Messrs Marsden-Jones and Turrill present the second Report on the Transplant Experiments at Potterne down to the end of 1931, and Mr C. G. T. Morison reports on the soils used and on analyses of some of the plants grown on them. Dr Illichevsky points out the importance of spring inundations in differentiating the floras of Russian river valleys. Miss Juby and Miss Pheasant present the results of an interesting and very complete study of intermittent germination in *Helianthemum guttatum*. The time lag and scatter in the germination of different samples of seed is astonishingly constant, and is shown to be due to the existence of two types of seed, "hard" and "soft," the latter, owing to their highly permeable testas, germinating within a few days, the former germinating at intervals for several months. Removal of the testas of the "hard" seeds resulted in immediate germination.

Four papers (including Mr Morison's already referred to) deal with problems connected with soil. Mr Gupta has studied the direct influence of soil density on the growth of various plants, and shows that it affects the underground parts much more than the shoots, leading to the formation of short thick rhizomes and roots, the effects of lack of aeration being excluded. Messrs A. S. Watt and G. K. Fraser write on "Tree roots and the Field layer," on the basis of instructive though incomplete experiments in Scottish woods. Messrs H. Godwin and J. S. Turner have studied the increase of soil acidity and of acidiphilous plants during succession from open water to forest at Calthorpe Broad, Norfolk. They show that this increase is marked, though forest is the outcome and not moor, as in the west.

Reviews include an "Autoreferat" by Dr H. Walter of Stuttgart on his theory of "Hydratur," with comments by Dr W. O. James; a review of Prof. Salisbury's important work on the East Anglian flora, by Prof. J. R. Matthews; a notice of Dr Rayner's reports on mycorrhiza in relation to forestry, and in *Citrus*; short notices of elementary books on ecology and on local flora and vegetation; and a review of the contents of the May issue of the *Journal of Animal Ecology*. There is also a notice of the collection of lantern slides, prints and negatives presented to the Society by Mr W. B. Crump.

Supplement XII of British Empire Vegetation Abstracts comprises 9 pages.

A. G. TANSLEY.

ZONATION IN THE SEA.

(1) **A. C. Stephen.** *Studies on the Scottish marine fauna: the natural faunistic divisions of the North Sea as shown by the quantitative distribution of the molluscs.* Trans. Royal Society of Edinburgh, 57, 601–16, 1933.

(2) **John Colman.** *The nature of the intertidal zonation of plants and animals.* J. Marine Biol. Ass. 18, 435–76, 1933.

(1) THE study of fisheries from an economic point of view and of the growth and numbers and migrations of fishes has far outstripped fundamental ecological work upon the animal and plant communities amongst which the fishes live and upon which they depend for food. In the end of the nineteenth century Hjort was working out the age distribution of the populations of Norwegian cod. It was not until 1911 that Petersen published the first quantitative studies of marine bottom animal communities, and not until after the War that other workers (Stephen, Hagmeier, and Davis), together with Petersen, extended these preliminary surveys to cover a large part of the North Sea area. The comparatively great resources of marine fishery research have enabled these four surveys to accumulate large series of results from quantitative sampling, most of which cannot be printed, although such full publication is of great importance for a proper criticism of the work and the complete application of it to fishery problems and to ecological theory. This circumstance is creditable to the scientific workers, but not to an industry whose annual turnover in the British Isles is probably over two thousand times the amount of money spent (by the Government) on fishery research. The present paper is a summary of the results of surveys in the northern parts of the North Sea, and touches Davis's survey in the south. It deals with Mollusca, for which the author has already published important data (*Trans. Roy. Soc. Edinb.*, 56, 291 and 521).

The work was mainly done between tide-marks, and at greater depths well beneath low-tide level, but a certain amount was done to connect these two zones of study. On the shore the main ecological divisions were found to be between sandy areas and muddy areas, sand occurring more on exposed coasts, while sand mixed with extraneous mud or interlayered with strong-smelling black mud was found in sheltered places, e.g. the Firth of Forth. On sandy habitats *Tellina tenuis* is the dominant lamellibranch, while on sand-cum-mud *Macoma baltica* and the cockle *Cardium edule* are the most abundant. At levels below this shore (intertidal) zone *Tellina* extends down to some 6 ft. below low-water mark. The author employs the term "littoral" to describe the region from high-water mark down to the limit of *T. tenuis*, but such a procedure seems perhaps rather arbitrary. Other molluscs have lower overlapping zones, e.g. *Donax vittatus* and *Tellina fabula.*

Coming to deeper levels, three zones or types of mollusc community are distinguished on the basis of the dominant species (meaning here the most abundant). It is not clear whether this result has been related to unpublished analysis of the zonation of the remaining members of the communities of animals, as would seem necessary if purely artificial communities are to be avoided. The coastal belt runs from littoral limits (6 ft.) down to about 120 ft. and is rich in molluscs. The offshore belt extends down to between 75 and 180 ft. and apparently is not entirely defined by its depths. The *Thyasira* (mollusc)-Foraminifera zone occurs in deeper waters to the north-east and again is rich in molluscs.

These results when mapped for the principal species show clearly how the shallow-water coast belts of the east of Scotland carry mollusc-zones similar to those of the Dogger Bank in the south, a fact summarised by the author in the statement that "the North Sea is best regarded as a large bay offset from the North-eastern Atlantic." He is to be congratulated on so neatly co-ordinating the results of four years intensive and arduous work with previous surveys and for clearing the way for further analysis of the extensive data already available for mapping the fish environments of the North Sea.

(2) The second survey noticed here covers in a more intensive way the relation of tidal habitats to the zonation of shore plants and animals. Four belt transects were made on Church Reef, which juts out in Wembury Bay at Plymouth. Exact profiles are published,

together with a description of the distribution of some of the main algae (eight species), one lichen, ten molluscs, and four Crustacea. The environment, though sheltered, is subject to surf action, which is shown to be an important factor in raising the effective height of "sea level" by 2 to 5 ft., so far as plants and animals are concerned. This splash zone is discussed in some detail, and the periodic limits of tide action are analysed in order to give accuracy to the definition of shore communities. The average curve for time and height of tide on the shore profile is somewhat complicated. The greatest numbers of species occur at low levels, and again at high levels, but the greatest concentration of the optimum ranges of species occurs in the intermediate zone. These results refer of course only to the common species studied. The author emphasises the desirability of using tidal data and not only heights as lines of reference for recording the occurrence of intertidal animals. Having thus accurately defined the zonation of various plants and animals (a thing which has seldom been properly done before, even in a small area like this), the author proceeds to discuss the problem of why the species have such definite zonation. It is pointed out that there are two modes of colonisation, first by passive dispersal as in algae and many animal larvae (e.g. barnacles), and the second by active movement (as in Gasteropod molluscs). The potentialities of the latter process appear to be much restricted by the clearly marked tropisms that such species possess. These tropisms have been studied by various workers (especially on *Littorina*), but it is not yet clear how much the reactions are really related to the adaptive optima of the animals and how far they limit species that could otherwise range much further. There is no very clearly marked separation in habitat between species of the same genus (e.g. *Littorina*), the ranges being characteristic but greatly overlapping. We are left therefore with a remarkably clear picture of an intertidal fauna, but as yet with no clearly seen reasons for the composition of the picture.

CHARLES ELTON.

SOCIAL INSECTS IN THE TROPICS.

Phil Rau. *Jungle wasps and bees of Barro Colorado Island* (*Panama*). 324 pp. (With numerous figures and an Appendix by J. Bequaert, describing new species of *Polybia*.) Published by the author, Kirkwood, Mo., U.S.A., 1933.

THIS book is mainly the fruit of Dr Rau's five weeks' visit in 1928 to the Barro Colorado Laboratory. The most important observations are those on the Stingless Bees (*Trigona* spp.) and on the Social Wasps (Polybinae and Polistinae). The Stingless Bees are an almost entirely tropical subfamily of which the species are extremely abundant and still very imperfectly known in South America. Their social life and the structure of their nests are in many ways unique and any additional information is very valuable. The Polybinae, again, are a subfamily of Social Wasps which is characteristic of South America where the species are very numerous. The classical works of von Ihering and Ducke have shown that the group is an extremely instructive one from the point of view of the taxonomist. Ducke's work, in particular, has shown that biological peculiarities—especially methods of nest construction— may indicate what structural features are of importance in the recognition of genera and species. Dr Rau has described and figured the nests of several species previously undescribed. His account, however, would have been more valuable if it had been brought more into relation with previous observations.

In dealing with the Polistinae, another group of Social Wasps, Dr Rau has been able to compare the habits of the tropical ones with those of temperate America, where his own observations are already well known. He is able to bring out a number of points of contrast, suggesting that adaptation to the environment has been considerable. In some of the solitary wasps, too, the author notes how behaviour is modified in relation to the sudden heavy rains of the tropical forest.

After a number of very miscellaneous observations on Arthropods encountered in Panama, there follows a chapter in which Dr Rau summarises several years' observations on the North

American Carpenter Bee, *Xylocopa virginica*. The species of this genus are interesting from their gregarious habits. Following Allee and Picard, we may believe that toleration of and interattraction between members of the same species have played a bigger part in the evolution of true social life than has usually been allowed. By contrast with social life, gregariousness has been insufficiently studied. Dr Rau's observations are therefore of considerable value. In the last chapter, the author summarises his views on the method of evolution. He attempts to harmonise the ideas of a number of writers, laying great stress on the importance of behaviour as opposed to structure. While there is sound sense in many of the points made, too many of the problems are either much more complex than the author indicates, or are provided with solutions that are largely verbal. Without a great advance in quantitative ecological technique, most of the questions raised cannot be answered. When we find that large numbers of a species have been killed off, it is not enough to say that the weaklings have been eliminated—we must actually demonstrate how far the statement is true. And so on with all the other assumptions which have to be made by anyone who puts forward a theory of evolution.

O. W. RICHARDS.

SCIENTIFIC COLLECTING.

R. M. Anderson. *Methods of collecting and preserving vertebrate animals.* Bulletin 69; Biological series 18. National Museum of Canada, Ottawa, 1932. Price 50 cents (cloth), or 25 cents (paper).

ANYONE who calls himself a collector is generally regarded with a good deal of suspicion and disapproval by modern biologists. Collecting has been a much abused hobby, resulting in needless massacre of vast quantities of "material" which can never be of the slightest scientific value. The collector often kills animals because they are there: the scientist only wants to collect with a definite object, and can only use other people's collections when they have been obtained and preserved in a scientific manner. Museums and systematists are all too familiar with the massive incompletely recorded collections of badly preserved animals obtained by travellers, explorers, and naturalists in all parts of the world. Mammals and birds are particular subjects for bad collecting, since the proper preservation of specimens is a far more difficult (or less known) job than it is with invertebrates. Although scientists may not approve of collectors in general they often have to collect animals for scientific work, and it is an undeniable fact that very few even first-class field biologists are masters of a really efficient technique for catching and preserving the animals they want. This book, therefore, should prove of the greatest value to biological science by showing straightforward methods for the collecting of vertebrates. Every intending collector, everyone who wishes to take advantage of peculiar opportunities for collecting, and every scientist who has need of specimens should have Anderson's book always available. He tells you in clear language, not only how to collect, but what, when, where, and why.

Details are given of methods of shooting and trapping large and small mammals and birds for scientific purposes. Both the well-equipped man who sets out with the intention of collecting and the casual traveller with no more apparatus than a pocket knife and a condensed milk tin are catered for in this section. The construction of simple and elaborate traps is explained, how and where to set them, and the right baits to use. The instructions given are never text-book quotations, but the practical experience of the author and other men who have done these things under all conditions and know all the unthought of snags which arise in field work. Perhaps it is in dealing with the animal after he has caught it that the collector mostly needs sound advice and experience. There are so many ways of skinning an animal, preserving its skull or skeleton, making prepared bird skins, etc., which can readily be carried out under leisurely conditions by the museum worker; but Anderson writes for the man who may be working alone in the open in all sorts of weather with the scantiest equipment, and who may need not only to make a scientific specimen of an animal but to eat it as well. The *essential* things to do in preserving, labelling, and measuring different types of

animals are clearly set forth, while more elaborate methods are described for those who have the facilities or wish to give particular attention to rare or valuable specimens. Anderson's advice on careful and systematic note-taking and labelling merits the attention of the most experienced field workers.

In addition to the detailed instructions on catching, preserving, labelling and transporting scientific specimens, hints are given on many useful things the collector can do with very little extra trouble. Records of the number of traps set, and animals caught per day per trap, may provide data on animal numbers of great value to ecologists. The collection of ecto- and endoparasites of many species when opportunity arises is another "sideline" of definite scientific importance, while collectors may hit upon outbreaks of disease among wild animals—a subject on which any data or material is valuable.

The ecologically minded reader of this book is very liable to contract a sudden inferiority complex, since he immediately realises the opportunities he has missed of contributing to biological knowledge. With Anderson as a pocket consultant he can be certain of making his field work yield results of wider and more permanent utility.

A. D. MIDDLETON.

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